# The influence of *Microhodotermes viator* nest density and dispersion on ecological processes

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## ABSTRACT

Heuweltjies are typically described as raised (± 2 m in height) circular earth mounds (5 – 30 m diameter) ubiquitous with the southern harvester termite (*Microhodotermes viator*), that occur in regular hexagonal patterns, predominantly in the north-western Succulent Karoo of South Africa, and are associated with distinct floral communities and faunal interactions. Most of the current literature on heuweltjies centres around their origins, of which two dominant theories persist. The termite origin theory is based on the strong association of heuweltjies with *M. viator* and their activities as ecosystem engineers that generate "*islands of fertility*" capable of initiating a cascade of events resulting in heuweltjie formation. Alternatively, the bush-clump theory posits that such "*islands of fertility*" necessary to initiate these events were generated by decomposing plant detritus. This study explores the ecosystem services (nutrient cycling, hydraulic soil properties, and biodiversity) provided by heuweltjies in a spatial-patterning context to assess these theories through remote sensing satellite and fieldwork of several sites across a rainfall gradient, *in situ* experimentation in Van Riebeeck Park (Worcester), and greenhouse experiments at the University of Cape Town. Novel findings include the quantification of termite faecal matter (frass) on heuweltjies and the associated enrichment in Worcester, and identifying a relationship between the distinct plant communities associated with heuweltjies and invertebrate density and richness from several sites. This study marks the first comparison of the spatial and productivity properties of heuweltjies between areas of high and low-densities, and found that these landscapes are similar, despite differences in density. This study also contributes to the current knowledge on the relationship between heuweltjie density and environmental conditions across a rainfall gradient and different biomes, as well as selective pressures that result in the distinct plant communities observed on heuweltjies. Experimental approach and specific aims of each data chapter are outlined here:

*Chapter 2* - The spatial properties and productivity of plots with high and low-densities of *M. viator* mounds were compared, and the relationships between their spatial properties and productivity values, as a function of density, investigated. Using Google Earth images paired plots of high and low densities of *M. viator* mounds were identified and their nearest neighbour distances and dispersion measures measured. High-resolution productivity data for these sites were obtained from the South African National Space Agency, and low-resolution productivity data from EarthExplorer for both autumn and spring to account for respective perennial and annual productivity. Although no clear relationship between spatial measures and productivity of the matrix could be determined, the spatial properties of

heuweltjies measured conform with the mechanism of regular pattern formation through termite foraging and competitive interaction.

*Chapter 3* – The enrichment of *M. viator* faecal matter (frass) was explored. Frass heaps deposited on superficial mounds were quantified (476 kg) and the mean enrichment of calcium (0.64 kg), carbon (64.4 kg) and nitrogen (3.65 kg) from these heaps calculated. These results were used to determine the enrichment levels of these nutrients. The nutrient profiles of frass, heuweltjie, and matrix soils were compared, and heuweltjie soils found to be more similar to frass (60 %) than matrix soils (58 %).

*Chapter 4* – Frass contributes to the enrichment of heuweltjie soils, however, construction and maintenance of nests by *M. viator* result in physical modification of soils. These physical and chemical differences between heuweltjie and matrix soils were quantified and compared and used for reciprocal greenhouse germination and growth experiments, which were supplemented with reciprocal *in situ* transplant and growth experiments. Germination trials tracked the germination and growth success of seeds from three plant species that occur predominantly on heuweltjies, and three that occur predominantly in the matrix. Germination was higher in heuweltjie soils for all seeds, however, two heuweltjie species had greater survival in heuweltjie soils than matrix soils. The reciprocal transplant experiment demonstrated significant transplant shock in seedlings and instead of growth, tolerance in different soil habitats was determined and species-specific tolerance responses were found for different organs of plants using multivariate regression models.

*Chapter 5* – Heuweltjies are typically associated with distinct plant communities. In this chapter I describe these distinct plant communities along with their matrix communities across a rainfall gradient and explore these relationships. In several field sites line transects were used to investigate plant communities by measuring species diversity and cover. Distinct plant communities on heuweltjies are often denser, attracting invertebrates as sites of dense food resources or refugia. In addition this chapter explores ant communities, as a representative taxon for invertebrates, and explores the relationship between community composition, diversity and biomass of ants with that of plant communities. Ants were collected via pitfall traps along the same transects used to measure plant communities. I found that heuweltjie plant communities are markedly distinct from that of their associated matrix communities. Ant communities on heuweltjies were not as distinct compared to ant communities in the matrix, however, plant biomass and species richness had a positive relationship with abundance and richness of ant species.

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# TABLE OF CONTENTS

**CHAPTER 4 – WHY DO NEST SYSTEMS OF *MICROHODOTERMES VIATOR* SUPPORT DISTINCTIVE PLANT COMMUNITIES?........ 68**

# CHAPTER 1 – INTRODUCTION

Heuweltjies (which is an Afrikaans word meaning "*small hills"*) are a conspicuous landscape feature observed as soil mounds between 4-32 m in diameter and 0.5-2.5 m high in the western parts of Southern Africa (McAuliffe *et al.*, 2014; Cramer *et al.*, 2017; Francis and Poch, 2019), for which the origins and nature continue to be the subject of much contention. Most of the earlier theories for their origin have been rejected, leaving two current competing hypotheses. Earlier hypotheses include mound formation through limestone faulting by which the limestone horizon of the Malmesbury shales have undergone calcretization following past faulting and folding (van der Merwe, 1944). Despite the spatial distribution of heuweltjies being associated with areas subject to increased natural seismic hazard (Fernández and Guzman, 1979) theories of the seismic genesis of heuweltjies following work on comparable mima-mounds (Berg, 1990) have been rejected based on the magnitude of earthquake required to produce such formations and patterns, the practicality of such models, and the internal stratigraphy of mounds which indicate successive deposition of sand layers over a significant temporal scale as opposed to a single seismic event (Moore and Picker, 1991). The regular dispersion of heuweltjies as opposed to clustering in areas of intense faulting is a further reason for the rejection of the faulting hypothesis.

Faunal genesis suggested by Lovegrove and Siegfried (1986) indicated that mounds are associated with termites (*Microhodotermes viator*) and mole-rats (*Cryptomys hottentotus*). The authors acknowledged the presence of structural components of termite mounds as part of heuweltjies, however, they attributed soil accumulation, and therefore heuweltjie growth and formation to lateral soil translocation by mole-rats that take up residence to avoid periodic flooding and water-logging (Lovegrove and Siegfried, 1986). However, mole-rats are absent from many heuweltjie sites (Milton and Dean, 1990) and also, little evidence to support such a theory was found when investigating excavated heuweltjies in Clanwilliam where mole-rat soil dumps were found to be tangentially rather than radially distributed from mounds (Moore and Picker, 1991). Moore and Picker (1991) found that the majority (78.9%) of intact mounds in Clanwilliam were currently inhabited by *M. viator*. The authors also found that the upper surface of inhabited mounds invariably had frass heaps, storage chambers and hives, while lower levels provided evidence of sub-fossil termite structures – indicating past and continual habitation by *M. viator* for at least 4000 years according to $^{14}$C dating of the excavated calcrete horizons.

Later $^{14}C$ dating, which also measured the associated values of organic and inorganic carbon, found the age of these calcrete horizons to be > 20 000 years (Midgley *et al.*, 2002) and questioned whether *M. viator* historically inhabited heuweltjies instead of another extinct species. This doubt was attributed to the size of heuweltjie mounds when compared to those of typical *M. viator* mounds and also the climate at the time of formation, being cooler, wetter and grassier during this time which is contrary to observed habitat preferences of *M. viator*. The authors instead proposed that heuweltjies were formed by an extinct termite species (possibly a *Macrotermes* sp.) that typically build larger epigeal mounds and are associated with climatic conditions similar to those prevailing at the time (Midgley *et al*., 2002). However, Picker *et al*. (2007) concluded that *M. viator* distribution is determined by rainfall and vegetative productivity as influenced by soil fertility and vegetation composition. The authors found that *M. viator* populations were in equilibrium with current climatic conditions as there was a positive relationship between mound density and rainfall. These results suggest that the fossil (lithified) structures in excavated mounds of Clanwilliam (Moore and Picker, 1991) could very well be those of *M. viator* (Picker *et al.*, 2007).

Cramer *et al*. (2012) proposed a vegetative origin for heuweltjies in Clanwilliam, Western Cape, involving differential erosion during the Pleistocene (Midgley *et al.*, 2002). They hypothesized that the bush clumps, which were regularly spaced due to competitive and facilitative interactions between plants, protected soils from erosion by producing contemporary raised "*islands of fertility"*. However, the authors failed to account for the absence of calcium carbonate horizons in some of the heuweltjies at the site previously dated by Midgley *et al*. (2002) who used this method - these horizons are characteristic and used for dating heuweltjies that would have suggested that these hardpans were relicts from past bush clumps formed through increased evapotranspiration and decreased leaching. This hypothesis was based on work on mima-mounds in San Diego (USA) (Barnes, 1879) where plant roots were proposed to protect soil from erosion, facilitating aeolian soil accretion in vegetation patches. This aeolian soil accretion hypothesis (Cramer and Barger, 2014) instead proposed that *M. viator* produces nutrient-rich islands that support denser vegetation, and that mounds grow with successive aeolian sediment deposition that would be trapped by the vegetation cover (McAuliffe *et al.*, 2014). There is convincing evidence indicating that *M. viator* is the initiator of a cascade of events that generate heuweltjies under specific conditions (presence of *M. viator*, local sediment source for aeolian deposition, rainfall and soil type) (Pringle and Tarnita, 2017; McAuliffe *et al.*, 2019). McAuliffe *et al.* (2019) described *M. viator* nests as having one of four physical manifestations; heuweltjies (sand-capped), cemented conical mounds, conical mounds and eroded heuweltjies, and no mound or heuweltjie, depending on local conditions. Consequently, sand-capped nests manifest patchily within the distribution of *M. viator* range. To differentiate these different nest phenotypes the broad term "*nest system*" is used throughout this thesis to describe *M. viator* hive and its associated soil modifications, and the term "*heuweltjie*" is reserved for only those nest systems that are capped by aeolian sand (McAuliffe *et al.*, 2019).

Heuweltjies (sand-capped nest systems of *M. viator*) occupy a large area (14-25 %) of the surface area where they occur in the Succulent Karoo, Nama-Karoo and Fynbos biomes, and their density was found to be significantly correlated with rainfall in the nutrient-rich Succulent Karoo part of their distribution (Picker *et al.*, 2007). The R-dispersion index, calculated using nearest neighbour distance, indicates a scale between perfect aggregation (R = 0) and perfect over-dispersion (R = 2.1491), and a value of 1 indicates a random dispersion pattern (Clark and Evans, 1954).

One of the more striking visual features of termite mounds is their over-dispersion especially in favourable habitats where they occur in high densities (Bourguignon *et al.*, 2011; Juergens *et al.*, 2015). Dispersion is a measure used to investigate the pattern of a population's spatial distribution, indicating whether it is aggregated, random or regular (Clark and Evans, 1954). For example, both active and inactive mounds of *Macrotermes michaelseni* analysed separately in the Okavango Delta were found to be randomly dispersed (Schuurman and Dangerfield, 1997). When the dispersion of active and inactive mounds was measured together in a single statistic, however, mounds were found to be significantly over-dispersed. Mounds of *Macrotermes bellicosus* in Southern Guinea savanna (Nigeria) were randomly dispersed, even with the inclusion of inactive mounds (Collins, 1981). The authors concluded that this was the result of the high mortality of young colonies predominantly as a result of predation. In addition, Korb and Linsenmair (2001) found that the distribution of these mounds was influenced by different processes depending on colony age. They conducted supplementary feeding experiments in which they found colonies with supplementary food had a 20-fold increase in size compared to colonies without supplementary feeding. They concluded that small, under-dispersed (aggregated) colonies become limited by food as the colony size increased, resulting in more intra-specific encounters and eventual over-dispersion (regular patterns) of surviving older, larger colonies (Korb and Linsenmair, 2001). These data, along with the findings of Picker *et al*. (2007) that heuweltjie density in homogenous vegetation types are positively correlated with rainfall and hence food abundance, support Laurie's (2002) assumption for over-dispersion if, under ideal conditions, colonies are resource- rather than predator-limited. Juergens *et al*. (2015) reviewed the over-dispersion of colonies of several social insects including that of the termite *M. michaelseni* (R = 1.54 and R = 1.3 respectively) in Outjo, Namibia (Turner, 2001) and Kruger National Park (Levick *et al.*, 2010; Cramer *et al.*, 2012). Namibian fairy circles associated with colonies of the termite *Psammotermes allocerus* have a dispersion index of 1.67 (Getzin *et al.*, 2015a; Getzin *et al.*, 2015b) and mapped colonies of the ant *Pogonomyrmex occidentalis* in Colorado were found to have a dispersion index of 1.37 (Wiernasz and Cole, 1995). This type of over-dispersion is considered to be the result of competitive interactions between colonies and provides a degree of stability and robustness to systems in response to increasing aridity acting as islands of enrichment that allow plants to persist longer than matrix-bound counterparts, and as a source for future propagules (Pringle and Tarnita, 2017). Specific soil conditions such as clay content and water holding capacity could further influence mound dispersion patterns (Cramer *et al.*, 2012). Over-dispersion has been demonstrated for *M. viator* in the Western Cape, South Africa (R-dispersion value ranging between 1.38 and 1.61) for all physical manifestations of *M. viator* mounds (Juergens *et al.*, 2015; McAuliffe *et al.*, 2018a) and comparable to that of nests of other social insects such as *Psammotermes allocerus* (1.67), *Macrotermes* spp. (1.54) and *Pogonomyrmex* spp. (1.37) (Juergens *et al.*, 2015).

Heuweltjies in Garies, Northern Cape were found to be over-dispersed (R = 1.56) (Juergens *et al.*, 2015), and this was supported by a broader study across the entire south-western distribution of Desert, Nama-Karoo, Succulent Karoo, Forest, Albany Thicket and Fynbos biomes (R = 1.27) investigating the role of vegetation induced aeolian soil deposition (Cramer and Midgley, 2015). The density of, and competition between mounds is positively correlated with available food resources (Levick *et al.*, 2010; Davies *et al.*, 2014a) and various models (Adams, 1998; Laurie, 2002; Tarnita *et al.*, 2017) propose that over-dispersion of colonies, as result of competitive intra-specific interactions, tend toward hexagonal arrays that completely partition the available space (Pringle and Tarnita, 2017). The dispersion mechanism illustrated for heuweltjies by Laurie (2002) describes a feedback loop between resource availability, foraging behaviour and intra-specific interactions, which is necessary to establish and maintain mound density and pattern over time (Laurie, 2002). This mechanism of central place foraging for *M. viator* and similar dispersion indices of heuweltjies when compared to other social insect colonies, including other manifestations of *M. viator* nest systems (McAuliffe *et al.*, 2019) supports the role of *M. viator* in heuweltjie genesis.

It is well known that mound-building insects such as ants and termites have profound effects on soil nutrients dynamics (De Bruyn and Conacher, 1990; Bignell, 2019) and that the nest systems are generally considered to be more nutrient-rich than adjacent soils (Bourguignon *et al.*, 2015). For example, *Macrotermes falciger* nest systems in Zimbabwe were found to have significantly higher concentrations of most measured macronutrients (Ca, K, Mg, $NO_3$ and S) and micronutrients (B, Co, Cu, Fe, Mn, Mo and Na), and contain significantly more clay particles than the adjacent soil (Seymour *et al.*, 2014). Similar trends have been recorded for nests systems and matrix soils of several termites including *Cubitermes niokoloensis* (C, N, $NH_4$ and $NO_3$), *M. bellicosus* (C, Ca, K, Mg, N, Na and P), *Macrotermes subhyalinus* (Ca, K, Mg and Na), and *Nasutitermes ephratae* (C, N, $NH_4$, $NO_3$ and P) (López-Hernández, 2001; Ndiaye *et al.*, 2004; Abe *et al.*, 2011; Tilahun *et al.*, 2012). A similar type of enrichment has been demonstrated for *M. viator* nest systems and matrix soils (the greatest enrichment observed in K, Ca, Mg, Mn and Fe) in the Worcester-Robertson Valley, South Africa (Midgley and Musil, 1990). Such localized enrichment has been found to significantly influence local floral communities (Okullo and Moe, 2012) resulting in increased landscape heterogeneity by establishing distinct plant communities on mounds compared to adjacent soils (Moe *et al.*, 2009; Erpenbach *et al.*, 2013). The role termites play as ecosystem engineers (Dangerfield *et al.*, 1998; McAuliffe *et al.*, 2019) through bioturbation affecting soil texture and porosity, and, together with foraging activities, soil nutrient content, means they can significantly influence plant biomass, productivity and species composition (Fox *et al.*, 2005; Davies *et al.*, 2014b; Joseph *et al.*, 2014). This thesis explores the spatial distribution and dispersion of *M. viator* nest systems across a rainfall gradient and the ecological implications of localized nutrient enrichment by *M.* viator in terms of the impact on the local floral and faunal community structure.

## 1.1. Factors affecting species distribution across different spatial scale

Few species are truly cosmopolitan in distribution, and many species currently have disjunctive populations which represent surviving remnants of a past, larger distribution pattern under different climatic conditions (Raven, 1972; Bakker *et al.*, 1995). Historic speciation events (driven through vicariance and active dispersal) are the primary drivers behind current, global species' distributions (Carlquist, 1983; Wiens and Donoghue, 2004; Trénel *et al.*, 2007). Dispersal models explain novel disjunctive populations across a pre-existing barrier, while vicariance models explain disjunctive populations through the appearance of a barrier across a former ancestral range (Platnick and Nelson, 1978). The appropriate model is assigned to a group based on the temporal distribution range and divergence from ancestors compared with the timing of historic tectonic events and whether or not the group has reasonable ability or means to cover the necessary distance and overcome obstacles (Raven, 1972).

Over and above these historical events that were largely responsible for current global distribution patterns of terrestrial biota, climate and soil are significant drivers of species distribution patterns at finer scales (Coudun *et al.*, 2006; Tromp-van Meerveld and

McDonnel, 2006; Gavin *et al.*, 2014). This is well-reflected in global vegetation patterns where six major forms of terrestrial vegetation are recognized (forest, woodland, shrubland, grassland, scrub and desert) which are further divided into 12 global terrestrial biomes based on physiognomy as a result of convergent evolution in response to climate and associated environmental conditions (Lomolino *et al.*, 2010). Community composition, local climate and major large-scale disturbance factors (e.g. fire) define plant species distributions at the regional scale of biome (Hoffmann *et al.*, 2012), which in South Africa are Albany Thicket, Desert, Forest, Fynbos, Grassland, Indian Ocean Coastal Belt, Savanna, Nama-Karoo and Succulent Karoo (Mucina and Rutherford, 2006). The Fynbos biome, for example, is defined primarily by climatic conditions of ca. 480 mm mean annual winter precipitation, natural disturbances (e.g. fire) and characteristic life-form patterns (proteoid, ericoid and restioid). This biome among others, supports the southern harvester termite (*M. viator*), the focus species of this study.

The Fynbos biome is divided into three vegetation types – fynbos, renosterveld and western strandveld – based on distinct vegetation composition and physiognomy resulting from steep edaphic differences. The fynbos vegetation includes plant communities adapted to grow mostly in nutrient-poor sandy soils derived from sandstone, quartzite and Tertiary sands of the Cape Fold Mountain Belt (Rebelo *et al.*, 2006). The renosterveld vegetation type is distinguished by plant communities that grow primarily in nutrient-rich shale soils. Renosterveld, however, can be found on other substrates except for sandstone and quartzite. Finally, the western strandveld vegetation type is defined by unique floral diversity reflecting plant biogeographic and geological patterns and typically occurs on coastal hinterland with stabilised Pleistocene dune cordons, but also on granites and Tertiary limestones. Thus, at the regional scale soil type appears to be a major determinant of plant species distributions (Richards *et al.*, 1997; John *et al.*, 2007). However, although this is primarily determined through historical and local soil-forming processes (Alexandrovskiy, 2007) biotic processes can also be an important factor in the development of soil types (Targulian and Krasilnikov, 2007). In this regard, termites and other soil-inhabiting organisms are well-known modifiers of soil (De Bruyn and Conacher, 1990; Bignell, 2019).

While animals are vagile and their community structure is largely determined by factors other than soil, many herbivorous animals (including the very large number of phytophagous insects) have a closer link to soil type via host plant dependency (Pienaar, 1974; Fryxell, 1991; Crist, 1998; Babin *et al.*, 2011; Gandiwa, 2014). Moreover, some herbivores can change plant communities and physical and chemical properties of soils through trampling, foraging, and deposition of faecal matter (Pastor *et al.*, 1998; Yoshihara *et al.*, 2010). Those animal species that have large, "*sessile*" and long-lived colonies – specifically social insects

– do have associations with different soil types in a similar fashion to plants (Lee and Wood, 1971b; Gertenbach, 1983; Meyer *et al.*, 1999; Kaakeh, 2005; Picker *et al.*, 2007) and also modify and enrich soils in the vicinity of their colonies (Moe *et al.*, 2009; Jouquet *et al.*, 2016). Given termite colony longevity and the high density of sessile mounds and their importance in ecosystem energy flux, their actions can significantly alter processes and community structure locally (Moe *et al.*, 2009; Erpenbach *et al.*, 2013). Termites often show well-defined distributions exclusive to particular soil types, horizons and particle size (Lee and Wood, 1971b). Higher densities of *Macrotermes* spp. mounds occur on sandy soils compared to granitic soils in northern Kruger National Park (Gertenbach, 1983; Meyer *et al.*, 1999). Sand termite (*Psammotermes hypostoma*) distribution is correlated with undisturbed yet sparsely vegetated, sandy substrates which are conducive for tunnel construction toward the water table to reach rapidly percolated water (Lee and Wood, 1971b; Roonwal and Bose, 1978; Kaakeh, 2005). In the case of the southern harvester termite (*M. viator*), soil fertility appears to predict distribution in the winter rainfall region, where the species is absent from fynbos vegetation associated with nutrient-poor soils but occurs in adjacent renosterveld which grows on nutrient-rich soils (Picker *et al.*, 2007; Cramer and Midgley, 2015). The first report of *M. viator* distribution (Coaton and Sheasby, 1974) indicates occurrence in three of Acocks' (1953) veld types; coastal tropical forest types, karoo and karroid types, and temperate and tropical forest scrub types of which contemporary counterparts are roughly Succulent- and Nama-Karoo and coastal sections of the Fynbos Biomes. It generally avoids the fynbos bioregion and sandstone geology (Picker *et al.*, 2004). This indicates that *M. viator* occurs predominantly in areas with mean annual rainfall between 125-750 mm in both winter and summer rainfall areas at altitudes up to 1675 m, which is a larger distribution range than that of heuweltjies (Coaton and Sheasby, 1974; Cramer and Midgley, 2015). This seemingly disjunctive distribution has been used as evidence against the a *M. viator* origin of heuweltjies (Cramer *et al.*, 2017).

Heuweltjies occur across 14-25 % (>67 309 km$^2$) of the Western Cape Province of South Africa (Lovegrove and Siegfried, 1986; Lovegrove and Siegfried, 1989; Moore and Picker, 1991; Cramer *et al.*, 2017). They occur predominantly in the Succulent Karoo Biomes (63 % of the total area), followed by the three bioregions of the Fynbos Biome (renosterveld, strandveld and fynbos), together constituting > 10 % of the area, and at < 10 % in the Nama-Karoo and Albany Thicket Biomes (Cramer and Midgley, 2015). These localities are generally characterised by winter rainfall regimes with summer droughts and relatively strong winds at < 1000 m elevations (Cramer *et al.*, 2017).

Midgley *et al*. (2002) cite an unpublished report by the Cape Department of Nature Conservation (Burgers, 1975) which found that heuweltjies were absent over an extensive region in the Western Cape (Caledon-Swellendam-Bredasdorp) where *M. viator* is present. Heuweltjie distribution occupies only 49% of the total distribution of *M. viator*, which raised questions concerning the causal role of *M. viator* in heuweltjie genesis (Cramer *et al.*, 2017). However, as discussed earlier, heuweltjies are only one of several manifestations of *M. viator* nest systems formed as a result of abiotic conditions that facilitate their genesis that may be absent or superseded at other locations across *M. viator* distribution where heuweltjies are absent (McAuliffe *et al.*, 2019).

## 1.2. Ecosystem engineering

The functional role of an organism in an ecosystem is described as comprising three essential features; diverting energy from the ecosystem towards its own productivity, its influence on the immediate physical environment, and its interaction with other organisms (Wood and Sands, 1978). An ecosystem engineer is defined as an organism with the ability to alter resource heterogeneity and volume in the landscape, thereby affecting species composition and distribution of other organisms (Dangerfield *et al.*, 1998; Wright *et al.*, 2002). Ecosystem engineers can be further distinguished as allogenic, modifying the physical state of living or non-living materials in their vicinity, or autogenic, modifying the ecosystem by their own physical structure (Jones *et al.*, 1994).

Well-known examples include bioturbation by earthworms (Darwin, 1892; Meysman *et al.*, 2006) which influence the physical properties of soil including aggregate stability, soil structure, and infiltration of water and aeration of deeper layers. By doing so, earthworms also affect biotic properties associated with soil such as microbial biomass and activity, nutrient cycling and mineralization and density of soil invertebrates (Eisenhauer *et al.*, 2007; Eisenhauer, 2010). In this way the earthworm *Lumbricus terrestris* also influences seed dispersal, burial, seedling recruitment, and the spatial distribution of seedlings, altering plant community composition (Milcu *et al.*, 2006). Colonization by birch (*Betula* spp.) in moorland is an example of an autogenic engineer which causes a decrease in light availability for the species-poor *Calluna vulgaris*-dominated understory (Mitchell *et al.*, 2007). This promotes an increase in species richness by including more shade-tolerant herbs and grasses (Hester *et al.*, 1991). In addition, the presence of birch has been found to significantly alter soil fertility by increasing pH, nitrogen mineralization rate, and exchangeable calcium and phosphorus concentrations as indicated from chronosequence studies (Mitchell *et al.*, 2007).

Dangerfield *et al*. (1998) demonstrated the importance of ecosystem engineering by the termite *M. michaelseni*. Their large (up to 4 m high with 50 $m^2$ basal area) epigeal mounds dominate the more xeric African savanna habitats, where they are distributed at densities between 0.005 and 6.01 $ha^{-1}$ (Schuurman and Dangerfield, 1996; Schuurman and Dangerfield, 1997). *M. michaelseni* central based foraging behaviour changes soil composition through mound construction and maintenance. Foraging can cover an area between 46 – 128 $m^2$ per night, extending up to 50 m from the nest. Between 1-1.5 tons/$ha^{-1}$ of plant material is translocated annually in this way to the nest (Lepage, 1979; Lavelle, 1997; Dangerfield *et al.*, 1998; Turner *et al.*, 2006) generating high concentrations of nutrients in centralized locations via decomposition of stored plant matter and accumulated frass (insect faecal matter). It is also possible that termites (with body-nitrogen content of 5.6-12.6%) that die in the colony or succumb to ant predation or competitive encounters with other termites on the nest mounds contribute to nutrient turnover and re-distribution (Matsumoto, 1976; Petersen and Luxton, 1982; Dangerfield *et al.*, 1998).

*Macrotermes* spp. modifies the physical soil properties and topography by non-random selection and relocation of soil particles for mound construction and maintenance (Dangerfield *et al.*, 1998). The nests are made by cementing together quartz particles with a mixture of termite saliva and clay minerals with high cation exchange capacities (Lee and Wood, 1971b; Dangerfield *et al.*, 1998; Jungerius *et al.*, 1999). Nutrient-rich soil (0.75-1.0 mm/$ha^{-1}$) is washed off nests annually by rainfall. Soil type and rainfall intensity determine how much soil is washed off, and it was estimated that in Uganda, 0.04 and 0.115 mm of modified clay-rich soil was annually washed off the surface of live and dead nests respectively, contributing to the nutrient enrichment of the landscape which in turn alters vegetation patterns (Pomeroy, 1976; Dangerfield *et al.*, 1998; Konaté *et al.*, 1999).

The amount of moisture and how long it is held in the soil influence microbial activity, and hence decomposition and nutrient cycling. In the Chihuahuan desert, Elkins *et al*. (1986) found that water infiltration rates decreased (51.3 ± 6.8 mm/$ha^{-1}$) in soils with little vegetation where termites had been absent for four years. They concluded that the absence of termites causes an increased soil bulk density as a result of soil backfilling and collapse of galleries, and subsequently decreased soil porosity (Elkins *et al.*, 1986). This type of ecosystem engineering is not restricted to characteristic epigeal termite mounds such as those constructed by *Macrotermes* spp. Many termites construct wholly subterranean nest systems (Lee and Wood, 1971b; Bignell *et al.*, 2011) while others have partially subterranean nest systems, with subterranean hives and low epigeal mounds. These "*lenticular*" mounds are often very large, but their ecosystem engineering role is poorly studied compared to the "*classic*" mounds of *Macrotermes* (Dangerfield *et al.*, 1998; Jouquet *et al.*, 2016) and *Trinervitermes* (Jouquet *et al.*, 2011; Jouquet *et al.*, 2016).

The first mention of *M. viator* as an ecosystem engineer (Hastings *et al.*, 2007) suggested that these sand-capped nest systems (heuweltjies) in the Succulent Karoo influence the physical and chemical environment which shape plant and animal communities (Kunz *et al.*, 2012) – but this suggestion was considered premature by McAuliffe *et al*. (2019), who subsequently produced a system dynamics model, discussed in section 1.4, describing several state transitions following colonization by *M. viator* that explain how different manifestations of nest systems are produced and how these influence local plant and animal communities (McAuliffe *et al.*, 2019).

## 1.3. Physical and biological characteristics of lenticular mounds

The term "*lenticular mounds*" was first coined by Darlington (1985) to describe very large disc-shaped soil mounds formed by termites (*Odontotermes* spp.) distributed over large areas across Kenya in over-dispersed patterns. These mounds are described as either bare or well-vegetated but are always associated with different plant communities and soil characteristics than those of inter-mound areas (matrix). The physical manifestation of four *Odontotermes* species nest systems was described as exhibiting "*classical*" lenticular mound structure (Darlington, 1985), and nest systems for all four species contained several fungus galleries where symbiotic fungi are cultivated (Darlington, 1997).

Materials used to construct termite nest systems are partially dependent on feeding habits and materials available but include soil particles, frass, saliva and plant debris (Lee and Wood, 1971b). As discussed in section 1.4 below, the physical manifestation of nests is influenced by environmental variables (Hesse, 1955; McAuliffe *et al.*, 2019), with the nest structure of a single species often assuming varying forms. This has lent some confusion to the debate on the nature of heuweltjies, one of the forms that *M. viator* nest systems exhibit (McAuliffe *et al.*, 2019). Unlike *Odontotermes* spp., however, *M. viator* does not cultivate fungus. It harvests a range of plant matter – including both fresh foliage and litter (Coaton and Sheasby, 1974; Francis *et al.*, 2013). Termites from all feeding groups (fungus growing, wood-, plant litter-, grass-, epiphyte-, and soil-feeding) are able to influence soil chemistry (Donovan *et al*. 2001; Ndiaye *et al*. 2003).

### 1.3.1. Nest system of the southern harvester termite

The *M. viator* nest system, when capped by sand (heuweltjies) most closely resembles that of *Odontotermes.* It ranges from partially epigeal bare mounds resembling classic termite mounds, through sparsely vegetated large discs to massive mounds that have a substantial vegetation cover, which often traps a thick layer of wind-blown sand (McAuliffe *et al.*, 2014). These and other layers were quantified by Moore and Picker (1991) who investigated water-eroded and intact *M. viator* mounds at Clanwilliam dam, Western Cape Province. Eroded mound dimensions were significantly smaller than intact mounds - (mean diameters of 12.31 and 15.88 m, and mean heights of 0.97 and 1.42 m for eroded and intact mounds respectively) because of the lack of the characteristic unconsolidated sand cover associated with this manifestation (heuweltjies) of *M. viator* mounds (McAuliffe *et al.*, 2019). The nest system comprises a large subterranean hive (diameter 15–30 cm, at depths 15–34 cm below the surface) which is capped with a partially epigeal mound (Moore and Picker, 1991). Under certain conditions, this is then covered by a thick sand layer (Coaton and Sheasby, 1974; McAuliffe *et al.*, 2019). Given the apparent considerable ages of many millennia of *M. viator* nest systems in the southern Succulent Karoo, there is some lithification of the soil in the close vicinity of the nest system (Moore and Picker, 1991; Midgley *et al.*, 2002; Potts *et al.*, 2009).

Moore and Picker (1991) detected typical termite nest structures in all of the heuweltjies where water erosion had removed the sand-capping. The unconsolidated sandy upper layer, which was absent on eroded mounds, contained fine calcified cracks and calcrete casts of termite tunnels (Moore and Picker, 1991). This network of tunnels consisted of narrow (3-10 cm diameter) anastomosing, tubular tunnels most densely concentrated in mound peripheries, with straight ellipsoidal tunnels extend radially from the central depression, through the mound periphery and several metres into the matrix. These act as highways from the central hive to matrix foraging areas and storage chambers (Coaton, 1962; Moore and Picker, 1991). Occurring close to the centralized depression and surrounding the hive are ovoid or kidney-shaped temporary storage chambers used for storing plant forage such as cut twigs. Such chambers have a highly polished internal surface exhibiting a calcified state of basal fossil layers in the Clanwilliam eroded mounds, with large openings as access tunnels. And finally, nest systems occupied by *M. viator* consist of horizontal shelves made from compacted organic matter, the dimensions of which were revealed in eroded mounds (Moore and Picker, 1991).

Soils associated with termite mounds typically have a high fine-clay particle (<20 µm) component (Konaté *et al.*, 1999), It has been demonstrated with detailed experiments and controls that *Odontotermes pauperans’* particle-size selection was dependent on the available soil and the constructions built, and if it was available finer particles were preferred (Jouquet *et al.*, 2002). By comparison, particle size analysis of soil samples (n = 7) collected at different depths below sand-capped *M. viator* nest systems (heuweltjies) revealed an average size distribution range of 10% clay (<2 µm), 50% silt (2-63 µm) and 40% sand (63-

1000 µm) (Francis *et al.*, 2013; Cramer *et al.*, 2016) according to the Wentworth grain size chart (Wentworth, 1922). Complementary analysis of matrix soils revealed a significant difference in the amount of silt present in mounds (50 %) compared to that of the matrix (36 %).

### 1.3.2. Influences of termitaria on community composition

It is well established that termite mounds have a strong influence on both plant and animal communities in their vicinity (Milton and Dean, 1990; Lovegrove, 1991). A change in plant community has been demonstrated in response to an extended, controlled absence of termites, leading to subsequent changes in primary consumer behaviour, on nest systems of an undisclosed subterranean termite species in New Mexico (Elkins *et al.*, 1986). Through their influence as ecosystem engineers, *Macrotermes* spp. in African woodland contribute to habitat heterogeneity by harbouring denser communities of woody plants and show more instances of mammal utilization than the matrix (Fleming and Loveridge, 2003; Joseph *et al.*, 2013; Joseph *et al.*, 2014). The age of *Trinervitermes trinervoides* mounds in the Free State, South Africa were found to be correlated with changes in the plant community (Smith and Yeaton, 1998). Active mounds were dominated by grasses *Tragus koelerioides* and *Themeda triandra* and subsequently replaced when mounds became inactive and/or eroded by *Eragrostis lehmanniana* and *Walafrida saxatilis*. Microbial communities in humid savanna are structured by termite presence and activity in humid savannas. The impact and extent were found to be species-specific when the impact of *Ancistrotermes* and *Odontotermes* were investigated (Jouquet *et al.*, 2005).

In the case of sand-capped *M. viator* nest systems (heuweltjies), the difference in plant communities is so distinct that colonies are readily detectable from afar as a result of the associated plant communities which contrast with those of the matrix e.g. the Worcester Veld Reserve (Western Cape) where *Aloe microstigma* (preferentially) and *Pteronia incana* (exclusively) grow on mounds, while *Gorteria integrifolia*, *Pteronia paniculata* and *Ruschia caroli* grow exclusively in the matrix (Rahlao *et al.*, 2008). Schmiedel *et al*. (2016) identified two distinct vegetation units occurring on heuweltjies in Namaqualand, those that are on the centre of the mound, and those on the fringe/buffer zone. Both differed from the matrix plant community vegetation. In grazed rangeland there was a decrease in annual plant cover and associated pH radiating outward from the centre of the mound, through the fringe and into the matrix, together with an increase of vegetation cover, species richness and perennial plant cover (Schmiedel *et al.*, 2016). However in an ungrazed (protected) site, perennial plant cover increased from the matrix to the centre of heuweltjies (Steinschen *et al.*, 1996).

Esler and Cowling (1995) showed that certain phenological characteristics exhibited by the mesembs (Aizoaceae) of the subfamily Mesembryanthemoideae at Tierberg in the southern Succulent Karoo better enabled them to exploit disturbed conditions on heuweltjies than the co-occurring subfamily Ruschioideae (Esler and Cowling, 1995). This was supported by long term (20 years) supplementary nitrogen trials at this same location where treatment of typical heuweltjie plant species (*Mesembryanthemum noctiflorum* and *M. vaginatum*), as well as typical matrix species (*Ruschia spinosa* and *Drosanthemum praecultum*) both, showed an increase in cover in response to soil nutrients (Seymour *et al.*, 2019). They suggested that it could be disturbance rather than soil nutrients that may have prevented the matrix species from growing on nutrient-rich heuweltjies.

Distinct on-mound plant communities and increased plant cover contribute to disturbance by attracting mammalian herbivores (Knight *et al.*, 1989; Midgley and Musil, 1990; Esler and Cowling, 1995; Kunz *et al.*, 2012; Schmiedel *et al.*, 2016), e.g., in the Karoo, sheep preferentially gaze on mound vegetation (Armstrong and Siegfried, 1990; Steinschen *et al.*, 1996), which may also be true for other grazers, such as steenbok, which also use the mounds as middens thereby contributing to nutrient-enrichment (Milton and Dean, 1990; Seymour *et al.*, 2019). Heuweltjies are also preferentially selected for burrowing due to softer soils and to make flood-proof dens for a range of animals including porcupines, aardvark (Louw *et al.*, 2017), foxes, moles, mongooses, rats, shrews, snakes, scorpions, lizards and beetles (Milton and Dean, 1990; Moore and Picker, 1991). While examining eroded mounds, Moore and Picker (1990) also discovered that mounds are often densely occupied by solitary soil-nesting bees, and web-building spiders have been found to occur at higher densities in more densely vegetated mounds than in the matrix (Henschel and Lubin, 2018). However, nothing is known about how mounds affect local invertebrate communities (explored in Chapter 5).

### 1.4. An integrated model for the development of lenticular mounds of the southern harvester termite and heuweltjie formation

The development of a large lenticular mound of *M. viator* (heuweltjie) would be initiated with the establishment of a colony from alates. Little is known about how young colonies establish in this species, although Moore and Picker (1991) recorded the size distribution of *M. viator* mounds at Clanwilliam, with the smallest cohort being 15.88 m in diameter. Subsequent colony growth would result in the accumulation of soil nutrients through central-based foraging and accumulated frass concentrated in the nest system. The resultant islands of fertility promote the development of denser vegetation cover which can act as a sediment trap for aeolian sediment (McAuliffe *et al.*, 2018a; McAuliffe *et al.*, 2019). In addition, bioturbation by termites (Cramer and Barger, 2014; McAuliffe *et al.*, 2014; Jouquet *et al.*, 2016) and other animals such as steenbok, ostrich, aardvark, and rodents (Armstrong and Siegfried, 1990; Milton and Dean, 1990; Milton *et al.*, 1992; Esler and Cowling, 1995; Louw *et al.*, 2017) that are attracted to such islands of fertility (Seymour *et al.*, 2014; Davies *et al.*, 2016) all improve soil permeability, aeration and soil-water relations (McAuliffe *et al.*, 2019). This creates a positive feedback between *M. viator* occupancy and mound maintenance and growth of the sand cap of mature heuweltjies. This seemingly simple mechanism, however, is complicated with the addition of external geographic variables of climate and aeolian sediment supply which determines the physical appearance of nests and areas in which heuweltjies manifest (Hesse, 1955; McAuliffe *et al.*, 2018b). It is of interest that Coaton and Sheasby (1974) never mentioned heuweltjies in the first detailed description of the nest system of *M. viator*, hence generating considerable confusion in the subsequent literature.

These transitions between physical and biological states and the effect of external variables are presented along with relevant feedback loops in a system dynamics model (McAuliffe *et al.*, 2019). The first state change is the establishment of a new colony in a place not occupied by a heuweltjie, and persistence in this vulnerable phase against predation, extreme climatic conditions and intra-specific competition with neighbouring colonies. The second state change is the modification of the soil nutrient profile (McAuliffe *et al.*, 2018b). Soils associated with heuweltjies showed generally higher levels of nutrients compared to that of the matrix (Midgley and Musil, 1990) in proportions similar to that of mounds of *M. bellicosus* (Abe *et al.*, 2011) and *M. falciger* (Muvengwi *et al.*, 2016) in comparison to associated matrix soils (Seymour *et al.*, 2014). The next transition is increased plant growth and productivity as a result of increased localized nutrient enrichment (section 1.3) (Midgley and Musil, 1990; Seymour *et al.*, 2019). Because mounds can persist in the landscape for millennia (Moore and Picker, 1991; Midgley *et al.*, 2002; Potts *et al.*, 2009; Cramer and Midgley, 2015) and the associated nutrient enrichment generates distinctive local soil modification, distinct floral and faunal associations develop on them (Esler and Cowling, 1995; Kunz *et al.*, 2012; Schmiedel *et al.*, 2016; Henschel and Lubin, 2018). Habitats with elevated soil nutrients harbour more deciduous plants than evergreen plants due to the higher nutrient requirements for leaf growth of the former (Chabot and Hicks, 1982; Midgley and Musil, 1990; McAuliffe *et al.*, 2014). Observed differences in mound vs. matrix plant communities of heuweltjies have long been ascribed to differences in nutrient profiles between the two habitats (Knight *et al.*, 1989; Armstrong and Siegfried, 1990; Midgley and Musil, 1990; Esler and Cowling, 1995; Rahlao *et al.*, 2008; Booi, 2011; McAuliffe *et al.*, 2018a; Seymour *et al.*, 2019) and this has also been demonstrated in other termite species (Dangerfield *et al.*, 1998; Muvengwi *et al.*, 2016). However as discussed below, mounds experiencing low rainfall may not develop any vegetation cover despite soil enrichment (McAuliffe *et al.*, 2019).

If vegetation growth is facilitated on mounds (as described above) then this affects further transitions. If precipitation is conducive to the development of denser localized vegetation to act as a sediment trap, the next transition involves aeolian sediment accretion (McAuliffe *et al.*, 2019). This transition is subject to wind and sediment supply. This state transition produces two feedback loops. One facilitates plant growth by creating favourable soil conditions for root growth, water infiltration and retention, as well as increased soil nutrients – as has been recorded elsewhere for desert plants (Soderberg and Compton, 2007). The second feedback loop ensures long term *M. viator* occupancy through improved resources (plant food material and reduced risk of predation as a result of the deeper location of the hive). This, in turn, establishes favourable conditions for new colonies, should the extant colony expire as it reinforces the previous state transitions (McAuliffe *et al.*, 2019). The final state transition involves increased faunal diversity and activity on mounds (Milton and Dean, 1990; Louw *et al.*, 2017) as animals are attracted to the greater plant productivity and deep, fine-grained soil for burrowing. The additional bioturbation and nutrient enrichment facilitated by increased faunal traffic generate two additional positive feedback loops that benefit plant growth and subsequent aeolian sediment accretion (McAuliffe *et al.*, 2019).

Three variables within this model of system dynamics determine the physical manifestation of *M. viator* mounds, they are; climate-dependant vegetation characteristics, aeolian sediment supply and distribution and, environmental and anthropogenic change. The first variable requires a structural response from the vegetation in response to nutrient enrichment generated by the presence of termites. Nutrient enrichment becomes concentrated and redundant, however, if it is not made available to local vegetation through adequate soil moisture levels, affected by rainfall events, as happens in other desert ecosystems (Noy-Meir, 1973; Hooper and Johnson, 1999). Thus the amount of biomass produced in response to local nutrient enrichment is correlated with mean annual rainfall. On the mesic end of the scale, nutrients have priority over rainfall. Current research suggests a middle ground or "*Goldilocks zone*" within which nutrient and moisture conditions are optimal for heuweltjie development (McAuliffe *et al.*, 2019). This explains why the presence of *M. viator* in the arid extremes is not generally associated with lenticular mounds, but rather manifests as small conical mounds or flat bare discs, without much above-ground evidence of mounds (McAuliffe *et al.*, 2019). In addition, vegetation directly surrounding nests in extremely arid regions is absent/reduced despite nutrient enrichment not only due to low rainfall but possibly also as a result of harvesting by the termites themselves, as observed in the sand termite (*Psammotermes allocerus*) in the Namib desert where it is considered to generate bare discs above the subterranean nests ("*fairy circles*") (Vlieghe *et al.*, 2015). Furthermore, in arid areas, mounds can be used to monitor the effects of grazing, as they are sensitive to preferential grazing that can clear mounds of perennial vegetation (Steinschen *et al.*, 1996; Stokes *et al.*, 2009), which prevents significant aeolian sediment deposition. By contrast, in mesic environments where *M. viator* occur and which provide localized nutrient enrichment, plant species compositions may change although the physical vegetation structure might not change enough to facilitate the formation of sediment traps, but aeolian sediment is distributed more uniformly across the landscape (McAuliffe *et al.*, 2019).

Differences in aeolian sediment supply can be correlated with heuweltjie size, evidenced by the observation of larger mounds in the Atlantic coastal plain region, presumably generated by more readily mobilized and fine-grained sediments (McAuliffe *et al.*, 2014). Quantitative analysis of aerial imagery across the entire distribution range of heuweltjies provides further evidence that mounds in areas with sparse vegetation, strong winds and summer droughts (typical of the Atlantic coastal plain) occupy a larger proportion of the landscape than those lacking these environmental variables (Cramer and Midgley, 2015). Floodplains may also act as a source of aeolian sediment where alluvial sediments are deposited. A positive relationship exists between the proximity to such floodplains and the proportion of the landscape covered by mounds (Cramer *et al.*, 2017). "*Capped mounds*" (resembling more typical termite mound structure) of *M. viator* occur only in certain regions although this was the nest system described as typical of *M. viator*, with no mention of heuweltjies (Coaton and Sheasby, 1974). McAuliffe *et al*. (2019) provide evidence for the persistence of these capped mounds of *M. viator* and why they do not develop into lenticular mounds. Mound persistence would be favourable in low relief areas where they are less susceptible to erosion by rainfall. This is evidenced by a site near Vanrhynsdorp where densely vegetated mounds persist at slope gradients of 2-5°, however, mounds at slopes of 6-14° are almost barren (McAuliffe *et al.*, 2019).

### 1.5. Thesis aims

This study aims to examine the processes and mechanisms by which fine-scale landscape heterogeneity is provided by the termite *M. viator*. Specifically, the thesis examines how *M. viator* nest systems generate local soil enrichment through frass accumulation, and how floral and faunal communities are influenced by the presence of the mounds. Their degree of dispersion and density in the landscape is also examined in relation to possible influences on ecosystem function, as measured by productivity.

*Chapter 2 – Effects of Microhodotermes viator nest density and dispersion on productivity:* Here the degree of primary productivity along a rainfall gradient affects various measures of *M. viator* nest system dispersion is explored. Specifically, as increasing rainfall is correlated with increasing plant productivity (Rutherford, 1980; Picker *et al*., 2007; McAuliffe *et al*., 2019; Seymour *et al*., 2019), nest diameter, density and degree of over-dispersion are expected to increase with increased rainfall as resources for colony success improve. Higher plant productivity might result in smaller foraging ranges (Laurie, 2002) of termite colonies and thus be associated with higher densities of mounds. This predicted foraging area would be maintained by intra-specific territorial interactions (Laurie, 2002; Picker *et al*., 2007) which are conventional determinants of colony spacing in social insects (McGlynn, 2012). Plant productivity on mounds is expected to have a unimodal distribution across the rainfall gradient, with the highest long-term rainfall areas having high, but similar productivity on both mounds and matrix sites, and lowest long-term rainfall plots having general lower productivity but with greater contrast between mounds and matrix site vegetation, as soils of *M. viator* nest systems have a higher water content than matrix soils (Midgley and Musil, 1990; Kunz *et al.*, 2012). Intermediate rainfall sites are expected to have the highest contrast between matrix and nest system sites, if one assumes that all nest systems of a similar size will have approximately equal frass production and soil enrichment, however, water is essential to mobilize these nutrients and make them available for plant uptake (Hooper and Johnson, 1999). In arid areas where water is the limiting resource, productivity in response to enrichment will only be visible when nutrients are mobilized by sufficient precipitation.

*Chapter 3 – Soil enrichment by Microhodotermes viator:* The mechanism for local soil enrichment by *M. viator* nest systems is examined, by comparing nutrient profiles of *M. viator* frass with that of nest system soils, and contrasting them with nutrient profiles of matrix soils. *M. viator* is probably unique amongst termites in depositing large volumes of frass on top of the nest system (Moore and Picker, 1991), providing a convenient and accurate way of measuring accumulated frass on nests and estimating its contribution to landscape fertility. The pathway of soil enrichment by frass is explored by examining leaching of bagged termite frass to matrix soils over a period of one year. The nutrient profile of *M. viator* frass is compared to that of soils associated with nest systems of other termite species providing supporting evidence for the hypothesis that *M. viator* generates heuweltjies by being the source of enrichment of heuweltjie soils that subsequently facilitate sediment accretion (Milton and Dean, 1990; Moore and Picker, 1991; Esler and Cowling, 1995; Laurie, 2002;

Mucina and Rutherford, 2006; Picker *et al.*, 2007; Francis *et al.*, 2013; McAuliffe *et al.*, 2019).

*Chapter 4 – Why do nest systems of Microhodotermes viator support distinctive plant communities?:* One of the striking features of heuweltjies specifically is their distinct plant communities, with most component plant species occurring mainly on heuweltjies and only a few matrix species occurring on heuweltjies (Esler and Cowling, 1995; McAuliffe *et al.*, 2018a; McAuliffe *et al.*, 2019; Seymour *et al.*, 2019). The proximate reasons for the uneven distribution of matrix and heuweltjie associated plant communities are explored through reciprocal field transplant experiments of seedlings, where the response variables of growth performance (root length, shoot length, number of branches/leaves, and qualitative health) are modelled against several potential explanatory environmental variables (soil nutrients, particle size, and soil-water dynamics) using multivariate multiple linear regression models for each species. Seedling transplant experiments examine the performance of mound species *Aloe microstigma*, *Pteronia incana* and *Tylecodon paniculatum*, and matrix species *Pteronia paniculatus* on both mounds and the matrix (Rahlao *et al.*, 2008). Additional experiments were conducted to observe reciprocal laboratory seed germination and *in situ* seedling growth of the above species to determine whether soil type has any influence on differential seed germination of heuweltjie vs. matrix species.

*Chapter 5 – Microhodotermes viator drives sharp gradients in floral and faunal communities:* Vegetation cover and floral community composition are examined for 10 sites across a rainfall gradient, to evaluate 1) how mound productivity varies in relation to rainfall (Fox *et al*., 2005; Picker *et al*., 2007) and 2) the relationship between productivity and plant community composition on heuweltjies (Davies *et al.*, 2014b; Pringle and Tarnita, 2017; Seymour *et al.*, 2019). Since certain mammalian species are known to be associated with *M. viator* nest systems (Milton and Dean, 1990; Lovegrove, 1991; Louw *et al.*, 2017) it is also possible that invertebrate communities might be structured by the presence of heuweltjies (Jouquet *et al.*, 2016; Henschel and Lubin, 2018). Ant diversity and abundance were used as an indicator of general invertebrate responses to habitat modification by *M. viator* communities. It is postulated that both plant productivity and diversity would be greater at high rainfall sites (Knapp *et al.*, 2002; Fox *et al.*, 2005) and that this may generate greater abundance and diversity of ant communities not only generally but specifically on nest systems vs. the matrix (Kaspari *et al.*, 2000; Delsinne *et al.*, 2010). Additionally, the contrast between measures of biotic productivity and diversity on matrix and nest system sites is expected to be greatest at intermediate rainfall sites, where the maximum contrast between productivity and vegetation cover is expected between nest system and matrix communities.

*Chapter 6 – Synthesis and general conclusion*: This chapter provides an integrated synthesis of the data presented to answer the research questions highlighted in the introduction of Chapter 1 with the existing literature. Support for an *M. viator* origin is proposed from various independent sources of data. This will lead to the development of a better understanding of the mechanisms by which certain manifestations of *M. viator* nest systems influence ecosystems (species richness, abundance and community structure) and how their physical and spatial properties respond to rainfall and productivity.

# CHAPTER 2 – THE EFFECTS OF *MICROHODOTERMES VIATOR* MOUND DENSITY AND DISPERSION ON PRODUCTIVITY

## 2.1. Introduction

Mobile organisms can move between and exploit favourable environments to escape climatic extremes or find new resource patches. They may also use different patches for different purposes, such as feeding or refugia (Wiens, 1976). Once established, sessile organisms, however, need to derive resources from their immediate vicinity. Most social insects (excluding nomadic Hymenoptera) are central-placed foragers, which means they must find and collect resources fairly near their fixed-position mounds (Brown and Gordon, 2000; Almeida *et al.*, 2018). For this reason, the spatial properties of social insect colonies match those of sessile organisms, with mound density being determined by the combined parameters of food, climatic conditions and soil properties (Lee and Wood, 1971b; Wiens, 1976; Picker *et al.*, 2007; Almeida *et al.*, 2018).

Vegetation type and cover influence the density and distribution of termite mounds (Lee and Wood, 1971b; Anderson *et al.*, 2016; Chakraborty and Singh, 2020) both directly as a food source and indirectly through their effects on the micro-climate. For example, mound temperatures of *Macrotermes bellicosus* mounds were found to be suboptimal in the shade of trees of closed gallery forests compared to open shrub savannas, which had a greater mound density than forests (Korb and Linsenmair, 1998). In contrast, *Macrotermes michaelseni* had greater densities in stable floodplain woodlands in the Okavango Delta, where mounds were protected from climatic extremes compared to the associated grassland habitats (Schuurman and Dangerfield, 1997).

Termites selectively utilise soil particles for mound construction (Jouquet *et al.*, 2002). Some species occur predominantly in sandy soils, which afford increased tunnelling and foraging efficiency (Pequeno *et al.*, 2015), while others typically prefer soils richer in clay that is used to construct their characteristic large mounds (Jouquet *et al.*, 2002; Abe *et al.*, 2012). In addition to soil type, soil-depth and water-logging influence termite density and distribution and represent a functional trade-off, so that different species of termite can co-exist in the same environments. For example in the Kruger National Park, South Africa topography and soil type differentially affected mound densities of several termite species (Meyer *et al.*, 1999; Levick *et al.*, 2010; Davies *et al.*, 2014a).

### 2.1.1. What drives termite mound dispersion?

One of the most dramatic visual aspects of termite mounds is their regular spatial distribution pattern across the landscape, although the biological factors underpinning this dispersion are poorly-studied. Termite mounds can be randomly distributed, under-dispersed (aggregated or clustered), or over-dispersed (regular dispersion). Considering termite mounds as spatial points, random distribution is described as an equal probability of any point occupying any space within a given area, without being influenced by any other point within or beyond this area (Clark and Evans, 1954). Under-dispersion patterns are not influenced by points within a given area, yielding clusters of points that can be either random or uniformly spaced together. Over-dispersion represents an optimal spacing whereby individual points are spaced at equal distances from six others forming a hexagonal pattern. Dispersion can be quantified either as R-dispersion with R-value equal to zero representing perfect under-dispersion, a value of one representing perfect random distribution, or perfect over-dispersion which is equal to 2.1491 (Clark and Evans, 1954). Alternatively, pair correlation function (PCF or $g(r)$) plots with $g(r)$ on the $x$-axis against distance ($r$) of any random point on the $y$-axis including 95 % simulation envelopes can be used to quantify dispersion. A $g(r)$ value = 1 represents random dispersion, >1 represents under-dispersion, and <1 represents over-dispersion (Wiegand and Moloney, 2013; Getzin *et al.*, 2015a). However, points of $g(r)$ beyond the 95 % envelope are also considered non-random (Wiegand and Moloney, 2013; Getzin *et al.*, 2015a).

In a review of mound dispersion and territoriality in ant communities, Levings and Traniello (1981) identified random distribution patterns in several ant species and a few cases of clumped/under-dispersion. Mounds of *Macrotermes* spp., *Cubitermes* spp., *Amitermes* spp., *Odontotermes* spp., and *Trinervitermes* spp. in northern parts of the Kruger National Park were found to have a clumped (aggregated) dispersion pattern across relatively homogenous environments. This was interpreted as being due to little competition (among thinly dispersed colonies) compared with an over-dispersed (regular) dispersion pattern were competition is high in the northern Kruger National Park (Meyer *et al.*, 1999) and the mounds are densely-distributed. However, every environment has a carrying capacity at which point competition is inevitable as densities approach this threshold (Begon *et al.*, 2006).

Over-dispersion has been recorded for several termite species (Collins, 1981; Benzie, 1986; Picker *et al.*, 2007; Cramer and Midgley, 2015; Getzin *et al.*, 2015a; Getzin *et al.*, 2015b) and quantified in terms of pair correlation functions, R-dispersion coefficients, hexagonal Voronoi tessellations, and nearest neighbour distances (Juergens *et al.*, 2015). Laurie (2002) proposed a model to explain the over-dispersion observed in *M. viator* under perfect homogenous conditions, which can be applied to other territorial termite species, noting that real systems do not conform to perfect homogeneity and subsequently that some degree of inconsistency is expected. The product of this model was an optimal, stable equilibrium between termite density and resources that tended toward an over-dispersed hexagonal array of predictable size, driven by intra-specific territoriality (Laurie, 2002). The spatial properties of fairy circles – the putative sub-surface mounds of the termite *Psammotermes allocerus* (Juergens *et al.*, 2015) – have been compared with mounds of several termites and one ant species (Table 2.1). All of these insect mounds had R-dispersion values consistent with over-dispersed patterns (R = 1-2.1491) with the highest value associated with Namibian fairy circles.

Aggression between neighbouring colonies is thought to underly over-dispersed mound patterns. In some species, this might be seen as overt physical aggression and in others, it is more subtle. For example, the sand termite (*P. allocerus*) is not considered an overtly aggressive species (Vlieghe, 2016), however, alternative intra-specific territorial interactions via terpenoid chemical defences are considered to act as a repellent, irritant and alarm pheromone in this genus (Krasulová *et al.*, 2012; Vlieghe, 2016). Intra-specific colony recognition and aggressive interactions between neighbouring colonies have been documented for *M. bellicosus* and *M. subhyalinus* either through aggression or by limiting contact with neighbouring colonies by blocking and segregating tunnels (Jmhasly and Leuthold, 1999a; 1999b). Survival of colonies of the ant *P. occidentalis* was negatively correlated with increasing nearest neighbour distance (Wiernasz and Cole, 1995) which can be ascribed to aggressive encounters between unrelated neighbouring colonies (Ryti and Case, 1984; 1992). There is some evidence for aggressive intra-specific interaction between colonies of *M. viator* (Coaton, 1958), on which Laurie (2002) based the model of over-dispersion through optimal transport in central place foragers.

**Table 2.1.** Summary of spatial pattern properties (mean number of Voronoi polygon sides, the mean percentage of Voronoi hexagons, mean nearest neighbour distance (NN), mean R-dispersion coefficient, and the highest g-value/maximum peak for *g*(*r*) and the associated distance on the x-axis (*r*) of pair correlation function figures) for several social insect species compared with vegetation self-organization – modified from Juergens *et al*. (2015).

| Species | Polygon sides | Hexagons (%) | Mean NN (m) | R-dispersion | *g*(*r*) | (*r*) |
|---|---|---|---|---|---|---|
| **Vegetation self-organization**[3] | 5,98 | 57 | 12,6 | - | 2,3 | - |
| ***Psammotermes allocerus***[2] | 5,97 | 46 | 16,26 | - | 1,6 | - |
| ***Psammotermes allocerus***[4] | 5,95 | 47 | 12,66 | 1,67 | 1,7 | 14,91 |
| ***Microhodotermes viator***[4] | 5,92 | 43 | 44,81 | 1,56 | 1,4 | 48,58 |
| **Vegetation self-organization**[4] | 5,9 | 47 | 57,59 | 1,52 | 1,2 | 67,7 |
| ***Pogonomyrmex* spp.**[4] | 5,87 | 34 | 10,88 | 1,37 | 1,3 | 17,3 |
| ***Macrotermes* spp.**[4] | 5,86 | 39 | 49,21 | 1,54 | 1,3 | 55,07 |
| ***Microhodotermes viator***[1] | 5,8 | - | - | 1,27 | - | 40 |
| ***Vegetation self-organization***[4] | 5,8 | 40 | 34,3 | 1,57 | 1,4 | 39,67 |

(Cramer and Midgley, 2015[1]; Getzin *et al*. 2015(a)[2]; Getzin *et al*. 2015(b)[3]; Juergens *et al*. 2015[4])

### 2.1.2. Termite induced ecosystem productivity

Termites are considered high to low-impact ecosystem engineers (Jones *et al.*, 1994; Dangerfield *et al.*, 1998; Jouquet *et al.*, 2006; McAuliffe *et al.*, 2019) modifying the physical and chemical properties of soils in their proximate environment. Physical changes are induced by the movement of selectively sized soil particles and construction of mounds (Jouquet *et al.*, 2002; Abe *et al.*, 2009), which often result in higher water infiltration and retention of soils (Lee and Wood, 1971b; Lamoureux and O'Kane, 2012; Jouquet *et al.*, 2016; Apori *et al.*, 2020), Chemical changes are the result of decomposition of termite faecal matter (frass) and stored food materials (Lee and Wood, 1971b; De Bruyn and Conacher, 1995; Brossard *et al.*, 2007), re-distribution of soils (Sarcinelli *et al.*, 2009), and decomposition of dead termites (Dangerfield *et al.*, 1998). All of these increase soil fertility and water-soil properties, which in turn increase local plant biomass and primary productivity (Elkins *et al.*, 1986; De Bruyn and Conacher, 1995; Sileshi *et al.*, 2010). These changes in the physical and chemical soil properties and the resulting increase in plant biomass are considered in Chapters 3–5. The term '*productivity*' in this thesis refers to primary plant productivity and is measured as Normalized Differnce Vegetation Index (NDVI) – calculated from the light reflectance of plants at certain frequencies determined from remote sensing data.

The focus of this chapter is the relationship between the spatial characteristics of *M. viator* mounds and primary productivity. Mounds of *M. viator* have been documented to occur at densities between 140 - 704 mounds per kilometre (mounds/km$^2$) at several sites and vegetation types (Picker *et al.*, 2007), with nearest neighbour distances between 40–55 m and a notably regular dispersion pattern (Lovegrove and Siegfried, 1989; Picker *et al.*, 2007; McAuliffe *et al.*, 2014; Cramer and Midgley, 2015). While termites can increase local productivity by modifying soils, their habitat preferences can also be influenced by existing vegetation productivity. For example, densities of mounds of several termite species (*Odontotermes* spp., *Macrotermes* spp., and *Trinervitermes* spp.) in the Serengeti National Park, Tanzania, were found to have a positive correlation with rainfall and greater herbaceous biomass (Anderson *et al.*, 2016). Picker *et al.* (2007) tested whether rainfall and primary productivity, measured as NDVI (Archer, 2004), correlated with the density and distribution of *M. viator* mounds across different vegetation types (Coastal Renosterveld, Fynbos, and Succulent Karoo) They found that mound density in the Succulent Karoo had a positive relationship with rainfall and NDVI, but no clear relationship was seen in Coastal Renosterveld or Fynbos vegetation types. In addition, there was a positive relationship for density with rainfall and mean annual rainfall (MAP) of mounds occurring on sites classified as high-fertility sites (Picker *et al.*, 2007). Later Cramer and Midgley (2015) found that vegetated earth mounds (heuweltjies -considered in this thesis to be *M. viator* mounds), occurred predominantly in the Succulent Karoo across NDVI values of 0.1–0.5. They also found that a smaller nearest neighbour distance was positively correlated with stronger over-dispersion and negatively correlated with increasing mound diameter (Cramer and Midgley, 2015). However, besides being the strongest predictor of mound presence within a range of 0.1-0.5 NDVI, they found no relationship between NDVI and spatial characteristics of *M. viator* mounds. Here I examine this relationship in greater detail to test whether productivity (or its proxy rainfall) can be associated with changes in mound density and size. While productivity on the large heuweltjies (± 20 m diameter for mature heuweltjies) is expected to be higher than the matrix as a results of termite contributions (Chapter 3), matrix productivity is unlikely to be influenced by the localised mound enrichment, so mound density might have an unrelated association with matrix productivity. These relationships are examined by isolating productivity (NDVI) values for mounds and matrix, in paired low and high density plots across a number of sites.

### 2.1.3. Objectives

This chapter examines the relationship between environmental variables (rainfall, productivity, and vegetation type) and *M. viator* mound density, nearest neighbour distance, and mound diameter. If primary productivity had any influence on *M. viator* density, then increased density, decreased nearest neighbour distance, and possibly smaller mound diameter (Cramer and Midgley, 2015) would be expected on more productive soils (matrix NDVI). Interestingly, despite occurring in renosterveld and western strandveld vegetation types of the Fynbos biome with more fertile soils, *M. viator* does not occur in the fynbos vegetation type which occurs on low-nutrient soils supporting vegetation with low foliar nitrogen (Picker *et al.*, 2004; Cramer and Midgley, 2015). This suggests that vegetation density and foliar nitrogen likely influence both the distribution as well as mound density of *M. viator*. Mounds of *M. viator* are considered "*islands of fertility*" (Cramer and Midgley, 2015; Cramer *et al.*, 2016; McAuliffe *et al.*, 2018a) because of the enrichment and improved soil-water properties resulting from the decomposition of termite frass (Midgley and Musil, 1990; Sarcinelli *et al.*, 2009), and the construction and maintenance of mounds (Lamoureux and O'Kane, 2012; Jouquet *et al.*, 2016) respectively. This has resulted in *M. viator* mounds often being more densely vegetated than the matrix and supporting greater plant diversity (McAuliffe *et al*. 2018a; 2019). The greatest sustainable density occurs in an over-dispersed hexagonal pattern – which has also been associated with greater ecosystem diversity and stability (Pringle *et al.*, 2010). Comparing productivity between paired plots of high and low-densities of *M. viator* mounds in homogeneous landscapes were expected to have greater densities of mounds in more productive plots. In addition, comparing productivity between mounds and matrix was expected to find that mounds increase landscape productivity.

## 2.2. Materials and methods

### 2.2.1. Compiling spatial data

Using Google Earth Pro (7.1.7.2606) a total of 38 remote sites were identified to collect data on density for dispersion analyses of *M. viator* mounds in the Albany Thicket, Fynbos (renosterveld) and Succulent Karoo Biomes (Mucina and Rutherford, 2006) (Figure 2.1). Two proximate 1 $km^2$ plots, one with a high and one with a low *M. viator* mound density (by count), were identified at each site (Appendix A). The Mean Annual Precipitation (MAP) of each site was calculated as the average from several years (2010 – 2018) of data collected from the nearest associated weather stations (SAWS, 2018). High and low-density plots were marked as polygons, and each *M. viator* mound visible in Google Earth Pro (7.1.7.2606) satellite imagery was marked with a circle. These data were imported into ArcGIS Pro (2.4.1.10048), where *x* and *y* coordinates of *M. viator* mounds were determined by plotting centroids of each mound and reporting the associated *x* and *y* coordinates as meters in the attribute table using the WGS 1984 UTM Zone 34S coordinate system. These data were used to calculate nearest neighbour distances, R-dispersion indices (Clark and Evans, 1954), pair correlation function (Wiegand and Moloney, 2013; Getzin *et al.*, 2015a) and produce Voronoi tessellations.

The R-dispersion index $(\bar{r}\mathrm{A}/\bar{r}\mathrm{E})$ was calculated for each plot respectively using the mean nearest neighbour distance ( $\bar{r}_{\mathrm{A}} = \Sigma r/N$) divided by the expected mean ( $\bar{r}_{\mathrm{E}} = 1/2\sqrt{\rho}$) if the distribution was random (*r* = measured nearest neighbour distance, *N* = number of observations, *ρ* = density of observations expressed as the number of individuals for the same measurement unit used for *r*) (Clark and Evans, 1954). An R-dispersion value of zero indicates complete aggregation, a value of one indicates random dispersion, and a value of 2,1491 indicates perfect regularity or over-dispersion. A Voronoi cell is the total area of the space closer to a particular point being analysed than any other point in the collective spatial point pattern. The '*dirichlet*' function in the R Statistical Software (version 3.6.1) Spatstat package produces a Voronoi tessellation of polygons in a two-dimensional plane which can be tabulated to show the number of polygons with a particular number of sides (Baddeley *et al.*, 2015). A greater degree of 6-sided Voronoi polygons is associated with a greater degree of regular dispersion (Clark and Evans, 1954; Laurie, 2002). Using this same package in

R Statistical Software (version 3.6.1), spatial distribution patterns were further characterised using pair correlation functions (PCF).

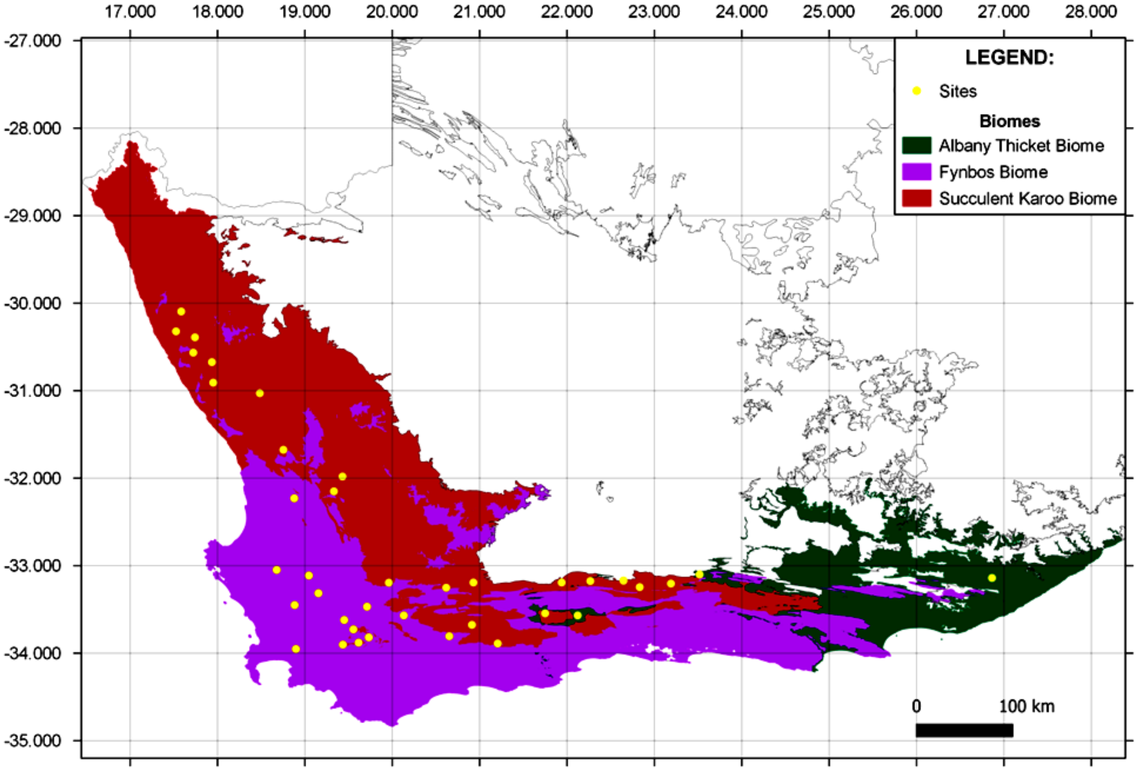

**Figure 2.1.** The distribution of 38 remote sites in the Albany Thicket, Fynbos (renosterveld), and Succulent Karoo biomes of South Africa.

The PCF or g(*r*) represents an average number of points within a specific distance (*r*) from a random point, where perfect random dispersion has a g(*r*) value of 1, and values <1 indicate regular dispersion while values >1 indicate clustering/aggregation (Wiegand and Moloney, 2013; Getzin *et al.*, 2015a). Plots of g(*r*) against (*r*) were produced (Appendix B) and included 95 % simulation envelopes of perfect random dispersion. The highest peak value of g(r) for each plot, along with the corresponding (*r*) value was recorded (Appendix A). G(*r*) extending beyond the 95 % simulation envelope is considered to represent regular dispersion/over-dispersion (Wiegand and Moloney, 2013; Getzin *et al.*, 2015a).

### 2.2.2. Compiling productivity (NDVI) data from different resolution scales

High resolution (1–2 m) SPOT 6 and 7 (*Satellite Pour l'Observation de la Terre*) satellite images ('old' imagery) were obtained at several intervals (*old*: August 2016 – October 2017, *new*: June 2018 – January 2020) for autumn (March-May, 2013 - 2018) and spring

(September-November 2013 – 2018) from the South African National Space Agency (SANSA) for all remote sites. Seasonal NDVI values were analysed with spatial characteristics to account for the different effects of perennial (autumn) and annual (spring) productivity. The available data of '*new*' datasets were incomplete, missing data for more than half of the new autumn (32/76) and spring (31/76) SPOT data, across the site distribution, years (2010-2017), and seasons (autumn and spring). The SPOT datasets (old and new as distinguished above) were thus supplemented (April 2020) with Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images (250 m resolution) from EarthExplorer (https://earthexplorer.usgs.gov/), from which a full complement of data for autumn and spring (2010 – 2017).

The SPOT (old) images were transcribed into raster images representing Normalized Difference Vegetation Index (NDVI) values in ArcGIS (2.4.1.10048). The mean NDVI was calculated from the value of all raster pixels within the polygon denoting each 1 km$^{-2}$ plot. The transcribed image was then clipped off the circles marking *M. viator* mounds and the mean NDVI of mounds calculated from values of each pixel within every circle at each site (positive). Finally, the mean NDVI of the matrix was calculated in the same way using the clipped (negative) original image without circles marking *M. viator* mounds.

For the SPOT (new) images, a different analytical approach was adopted that was more efficient in handling the increasing bulk of data. The available images were merged into a single image (QGIS, 3.8.1) for autumn and spring, respectively. The resulting images were processed and NDVI calculated in R Statistical Software (version 3.6.1) using the packages '*caret*' (Kuhn *et al.*, 2020), '*e1071*' (Meyer *et al.*, 2015), '*raster*' (Murrell, 2011) and '*rgdal*' (Bivand *et al.*, 2015). Mean NDVI values for plots, mounds and adjacent matrices at each remote site for autumn and spring were determined from several random points within each polygon boundary. The extracted NDVI data were exported to Excel for manipulation and further analyses in R Statistical Software (version 3.6.1).

There was no need to calculate NDVI for the MODIS images since these data were already available in the raster pixels of the images obtained from EarthExplorer (https://earthexplorer.usgs.gov/). The images were merged into a single image in ArcMap (10.6) and the NDVI raster data scaled by a factor of 10 000 to convert these values within the normal NDVI range (between -1 and 1). Mean NDVI values for plots, mounds and matrices at each remote site were determined from several random points within each polygon boundary, and these data exported to Excel for further manipulation and analyses in R Statistical Software (version 3.6.1).

Multi-year, resolution-scale Pearson product-moment correlation and regression analyses of NDVI were determined to assess the quality of datasets. A significant positive correlation was expected between the different NDVI datasets (MODIS and both, old and new SPOT), though correlation would likely be weak between high-resolution SPOT datasets (old and new) and low-resolution MODIS datasets. Lack of such correlation would indicate considerable discrepancy that should be taken into account for future comparative studies. All data points available for autumn and spring, respectively, were correlated for each year. Data points that carried over into multiple years were also correlated over these periods.

### 2.2.3. Statistical analyses

The difference in NDVI between high and low-density plots was investigated with two-way Analysis of Variance (ANOVA) with factors density (high or low) and habitat (matrix or mound) using all the available NDVI datasets (MODIS and both old and new SPOT) to identify differences in outcome based on different resolutions. Two-way ANOVA models were subjected to pairwise posthoc analysis using Tukey adjustment. The MODIS and new SPOT data set compared mounds and matrices in both autumn and spring seasons to accommodate for annual productivity.

The difference between values from high and low-density plots for mean nearest neighbour distance, R-dispersion coefficients, frequency of hexagons (%), number of sides in two-dimensional Voronoi tessellations, and mound diameter was tested using the appropriate test of means (Student T-test or Mann-Whitney U). To get a sense of the correlation of variables a correlation matrix (Harrell and Harrell, 2015) was produced (Appendix C), where the correlation was measured with Pearson’s product-moment correlation and regression analyses.

Using these and additional environmental data (rainfall, biome, bioregion, and vegetation unit), and autumn and spring NDVI of the matrix respectively from different productivity datasets, multiple multivariate linear regression models were produced to explain the observed variation in density and dispersion of *M. viator* mounds across a rainfall gradient. The magnitude of influence of rainfall and both autumn and spring NDVI from respective productivity datasets on density and dispersion were quantified to establish which of these variables played a greater role in observed densities and dispersion patterns. The basic model structure was:

$$DE = m + m(\text{Rcoef}) + m(\text{NN}) + m(\text{Hex}) + m(\text{Diameter}) + m(\text{MAP}) + m(\text{NDVI}) + m(\text{Biome}) + m(\text{Bioregion}) + m(\text{Vegetation unit})$$

In the equation, the influence of variables on the observed density (DE) is equal to the sum of the model intercept coefficient (m) and the product of variables with their respective coefficients. The variable means used in the equation are dispersion (Rcoef), nearest neighbour distance (NN), percentage hexagons in the Voronoi tessellation (Hex), mound diameter, rainfall (MAP), either spring or autumn productivity (NDVI) respectively, and the biome, bioregion, and vegetation unit which have all been given numeric values (Appendix D). The same model is used to test the influence of variables on dispersion, substituting dispersion in place of density, and density in place of dispersion.

## 2.3. Results

### 2.3.1. Density and diameter of *M. viator* mounds

Across all sites, *M. viator* mounds had a mean density of 235 ±128 mounds/km$^2$ and a diameter of 23.88 m (±5.18). High-density plots had a significantly higher number of mounds compared to low-density plots (Table 2.2).

**Table 2.2.** The mean (± standard deviation) density and diameter of *Microhodotermes viator* mounds ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Mann-Whitney U).

| Variable | All | High-density | Low-density |
|---|---|---|---|
| **Density (mounds/km$^2$)** | 234,50 (±127,90) | 308,95 (±131,68)*** | 160,05 (±66,59)*** |
| **Mound diameter (m)** | 23,88 (±5,18) | 24,31 (±5,98) | 23,44 (±4,27) |

There was no significant correlation of density with mean annual precipitation (MAP) when high and low plots were grouped together ($p$ = 0.082), or when plots were analysed separately as high ($p$ = 0.086) and low-density plots ($p$ = 0.187). There was also no significant relationship between total, low, or high-densities with any of the NDVI datasets or seasons viz.: **1)** No significant relationship with low-resolution (MODIS) autumn ($p$ = 0.328) or spring NDVI ($p$ = 0.571) when plots were grouped together, or when analysed separately for high (autumn, $p$ = 0.444; spring, $p$ = 0.752) and low-density plots (autumn, $p$ = 0.345; spring, $p$ = 0.494); **2)** No significant relationship with the old, high-resolution (SPOT) autumn productivity ($p$ = 0.688) when plots were grouped together, or when analysed separately for high ($p$ = 0.576) and low-density plots ($p$ = 0.801); **3)** No significant relationship with the new, high-resolution autumn ($p$ = 0.443) or spring productivity ($p$ = 0.496) when plots were grouped together, or when analysed separately for high (autumn, $p$ = 0.695; spring, $p$ =

0.640) and low-density plots (autumn, *p* = 0.226; spring, *p* = 0.113). There was no significant (*p* = 0.4465, Mann-Whitney U) difference between mound diameters of high and low-density plots (Table 2.2). However, mound diameter had significant positive relationships with new high-resolution (SPOT) NDVI values across for autumn of *M. viator* mound density treatments (all, cor = 0.55; high-density, cor = 0.60; low-density, cor = 0.54) and spring (all, cor = 0.68; high-density, cor = 0.68; low-density, cor = 0.73) but had a significantly negative relationships with older autumn SPOT values in the treatments with all plots considered together (cor = -0.36), and when only low-density plots were considered (cor = -0.45).

### 2.3.2. Productivity of *M. viator* mounds and associated matrices

There was a significant, positive relationship between low-resolution (MODIS) and new high-resolution (SPOT) spring productivity (cor = 0.42), and a significant, negative relationship between the old and new autumn SPOT productivity datasets (cor = -0.37). Both the low-resolution (MODIS) autumn and spring productivity (NDVI) had significant positive relationships with overall rainfall (MAP). However, both new high-resolution (SPOT) autumn and spring NDVI had significant negative relationships with MAP overall, and in the Succulent Karoo.

According to low-resolution MODIS datasets matrix habitats had a similar autumn NDVI compared with *M. viator* mound habitats (Table 2.3). NDVI was higher in high than low-density plots. The two-way ANOVA however found that these differences were not significant along any combination of factors habitat (*p* = 0.9152), density (*p* = 0.8646), or the interaction between them (*p* = 0.9683). Similarly, spring NDVI was similar in matrix habitats and mound habitats and slightly higher in high than low-density plots (Table 2.3), but was also not significant along any combination of factors habitat (*p* = 0.9777), density (*p* = 0.8877), or the interaction between them (*p* = 0.9849).

**Table 2.3.** The mean (± standard deviation) productivity measured as Normalized Difference Vegetation Index (NDVI) of matrix and *Microhodotermes viator* mound habitats, and high- and low-density plots.

| | Matrix | Mounds | High-density | Low-density |
|---|---|---|---|---|
| **MODIS (autumn)** | 0,2597 (±0,0879) | 0,2581 (±0,0868) | 0,2609 (±0,0825) | 0,2580 (±0,0948) |
| **MODIS (spring)** | 0,2497 (±0,1049) | 0,2494 (±0,1030) | 0,2511 (±0,1022) | 0,2478 (±0,1088) |
| **SPOT (old, autumn)** | 0,1283 (±0,0318) | 0,1300 (±0,0392) | 0,1291 (±0,0290) | 0,1281 (±0,0327) |
| **SPOT (new, autumn)** | 0,1832 (±0,0814) | 0,1901 (±0,0706) | 0,1845 (±0,0700) | 0,1828 (±0,0891) |
| **SPOT (new, spring)** | 0,2641 (±0,0875) | 0,2771 (±0,0736) | 0,2651 (±0,0814) | 0,2693 (±0,0893) |

The high-resolution SPOT data (old and new) however, found that mound habitats had higher autumn NDVI than the associated matrices (Table 2.3). Autumn NDVI was also slightly higher in high- than low-density plots (Table 2.3). For both old and new data these differences, however, were not significant along any combination of factors habitat (old, $p$ = 0.4580; new, $p$ = 0.6496), density (old, $p$ = 0.8317; new, $p$ = 0.9724), or the interaction between them (old, $p$ = 0.1820; new, $p$ = 0.7807).

Mound habitats had somewhat higher spring NDVI values than matrix habitats, for which there were only new SPOT data to compare (Table 2.3). Mean spring NDVI values were similar on mounds in low and high-density plots (Table 2.3). This difference, however, was also not significant along any combination of factors habitat ($p$ = 0.7886), density ($p$ = 0.8265), or the interaction between them ($p$ = 0.9462).

### 2.3.3. Mound density and nearest neighbour distance

The mean nearest neighbour distance (NN) across all sites and plots was 46.93 (±10.08) m. As expected, low-density plots had a significantly larger NN compared to high-density plots (Table 2.4). Nearest neighbour distance had significant negative relationships with both spring (cor = -0.31, $p < 0.01$) and autumn (cor = -0.33, $p < 0.01$) low-resolution productivity (MODIS) when all plots were measured together. This was also true for the relationships with MODIS autumn (cor = -0.48, $p < 0.01$) and spring (cor = -0.47, $p < 0.01$) with low-density plots.

**Table 2.4.** The mean (± standard deviation) nearest neighbour distance between mounds of *Microhodotermes viator* in high- and low-density plots ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Mann-Whitney U).

| | **High-density** | **Low-density** |
|---|---|---|
| **Nearest neighbour distance (m)** | 41,84 (±6,85)** | 52,02 (±10,28)** |

### 2.3.4. R-dispersion coefficients

The R-dispersion coefficients of all treatments (total, and high and low-density) were over-dispersed (0 </= aggregated; 0-1 = random dispersion; 1-2.15 = overdispersion; Clark and Evans, 1954). The mean R-dispersion coefficient across all sites and plots was 1.066 (±0.217), and was higher in high density plots, and lowest in low-density plots (Table 2.5). However, this difference was not significant ($p$ = 0.2373, Mann-Whitney U). R-dispersion

values had significant negative relationships with low-resolution (MODIS) autumn productivity in all plot density treatments: **1)** Total density (cor = -0.43, $p < 0.001$); **2)** High density (cor = -0.34, $p < 0.05$); **3)** Low density (cor = -0.53, $p < 0.001$). While only total (cor = -0.42, p < 0.01) and high density (cor = -0.59, $p < 0.001$) plots had significant negative relationships with spring MODIS productivity.

**Table 2.5.** The mean (± standard deviation) R-dispersion coefficients of high- and low-density plots of *Microhodotermes viator* mounds.

| | **High-density** | **Low-density** |
|---|---|---|
| **R-dispersion coefficient** | 1,074 (±0,235) | 1,058 (±0,200) |

### 2.3.5. Voronoi polygons of low and high density mounds

The overall mean number of sides of two-dimensional Voronoi polygons was 5.81 (±0.08) and was similar to that of high and low-density plots (Table 2.6). The frequency of hexagonal polygons, however, was significantly higher in high than in low-density plots (Table 2.6). The total mean frequency of hexagonal polygons was 35 (±5) %. No relationships of hexagon frequency or polygon side number were detected with any of the productivity values. However, *M. viator* mound density had significant positive relationships with both the frequency of hexagons (cor = 0.46, $p < 0.001$) and the number of sides (cor = 0.24, $p < 0.05$) in two-dimensional Voronoi polygons. The relationship of density with frequency of polygons was reflected in high (cor = 0.43, $p < 0.01$) and low-density plots (cor = 0.36, $p < 0.05$).

**Table 2.6.** The mean (± standard deviation) of the frequency with which hexagons occur and the mean number of sides per polygons in the Voronoi tessellation of *Microhodotermes viator* mounds at different densities ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Student T-test).

| | **High-density** | **Low-density** |
|---|---|---|
| **Hexagon frequency** | 36 (±4) % ** | 33 (±5) % ** |
| **Mean number of sides/polygon** | 5,81 (±0,07) | 5,80 (±0,09) |

### 2.3.6. Pair correlation function *g*(*r*) peak and its distance (*r*)

The mean *g*(*r*) and (*r*) values of all sites and plots were 2.183 (±1.340) and 59.571 (±16.388), respectively. The mean *g*(*r*) of high- and low-density plots did not differ significantly ($p = 0.9657$, Mann-Whitney U), nor was the difference in (r) between high- and low-density plots significant ($p = 0.3352$, Mann-Whitney U) (Table 2.7). All values of $g(r)$ were >1 indicating clustering/aggregation, with no random ($g(r) = 1$) or regular dispersion ($g(r) < 1$; Wiegand and Moloney, 2013; Getzin *et al*. 2015). The $g(r)$ had significant positive relationships with low-resolution (MODIS) productivity values in both autumn and spring across all *M. viator* mound density treatments, as well as a significant positive relationship with high-resolution (SPOT) autumn productivity when all plots were measured together (cor = 0.42, $p < 0.05$). The $g(r)$ in all density treatments had significant positive relationship with low-resolution (MODIS) autumn (total, cor = 0.42, $p < 0.001$; high-density, cor = 0.37, $p < 0.05$; low-density, cor = 0.49, $p < 0.01$) and spring (total, cor = 0.48, $p < 0.001$; high-density, cor = 0.40, $p < 0.05$; low-density, cor = 0.58, $p < 0.01$) productivity. The distance ($r$) of these peaks, however, had significant negative relationships with both autumn (total, cor = -0.36, $p < 0.01$; low-density, cor = -0.36, $p < 0.01$) and spring (total, cor = -0.46, $p < 0.01$; low-density, cor = -0.51, $p < 0.01$) MODIS productivity at total and low-density treatments.

**Table 2.7.** The mean (± standard deviation) of the pair correlation function peaks $g(r)$ and the corresponding distance of peaks ($r$) for sites with a high- and low-densities of *Microhodotermes viator* mounds.

| | High-density | Low-density |
|---|---|---|
| **PCF peak or *g*(*r*)** | 2,159 (±1,464) | 2,207 (±1,220) |
| **Peak distance (*r*)** | 57,387 (±15,143) | 61,756 (±17,473) |

### 2.3.7. The influence of vegetation type on spatial parameters of *M. viator* mounds

The 38 pairs of plots (high and low-density) consisted of three pairs (n = 6) from the Albany Thicket, 11 pairs (n = 22) from the Fynbos, and 24 pairs (n = 48) from the Succulent Karoo biomes (Table 2.8). As expected the Succulent Karoo had a greater density of mounds compared to the Fynbos, however, it was interesting to find the greatest mean density in the Albany Thicket, though this is probably due to the small sample size and high variability. The expected inverse of the latter was true for nearest neighbour distance. It was interesting to find over-dispersion only in the Succulent Karoo compared to the other biomes that were under-dispersed. For low-resolution (MODIS) and the old high-resolution (SPOT) productivity (NDVI) datasets, the arid and sparse Succulent Karoo, as expected, had the lowest NDVI compared to both the Albany Thicket and Fynbos, however, the mean NDVI for the Succulent Karoo according to new SPOT data were greater than the Albany Thicket. Unfortunately, the missing data from the incomplete SPOT NDVI included that of all Fynbos sites and were thus not able to be compared.

**Table 2.8.** The mean (± standard deviation) spatial properties of *Microhodotermes viator* mounds and associated autumn and spring productivity (MODIS and SPOT) values from the Albany Thicket, Fynbos, and Succulent Karoo biomes, including density, mound diameter, nearest neighbour distance, R-dispersion coefficient, percentage of hexagonal polygons in Voronoi tessellations and number of sides per polygon, greatest pair correlation function peaks g(*r*), and the corresponding distance of peaks (*r*). Largest measures in red, and lowest in blue.

| Variable | Albany thicket | Fynbos | Succulent Karoo |
|---|---|---|---|
| **Density (mounds/km$^2$)** | 298,50 (±223,92) | 163,81 (±58,45) | 248,33 (±123,63) |
| **Mound diameter (m)** | 20,80 (±3,09) | 22,77 (±2,41) | 24,55 (±5,79) |
| **Nearest neighbour distance (m)** | 43,45 (±8,62) | 48,05 (±6,94) | 46,98 (±11,01) |
| **R-dispersion coefficient** | 0,9391 (±0,4523) | 0,9578 (±0,2527) | 1,1200 (±0,1474) |
| **% Hexagons** | 35,28 (±4,71) | 33,98 (±4,74) | 35,06 (±4,93) |
| **Mean number of sides/polygon** | 5,81 (±0,1) | 5,80 (±0,10) | 5,81 (±0,07) |
| **PCF peak or *g*(*r*)** | 1,72 (±0,25) | 3,17 (±2,56) | 1,94 (±0,55) |
| **Peak distance (*r*)** | 58,20 (±21,92) | 61,53 (±17,97) | 59,14 (±15,55) |
| **MODIS (autumn)** | 0,3425 (±0,0838) | 0,3314 (±0,0985) | 0,2283 (±0,0625) |
| **MODIS (spring)** | 0,2828 (±0,0828) | 0,3554 (±0,1297) | 0,2148 (±0,0702) |
| **SPOT (old, autumn)** | 0,1719 (±0,0226) | 0,1274 (±0,0307) | 0,1249 (±0,0352) |
| **SPOT (new, autumn)** | 0,1621 (±0,0629) | - | 0,1920 (±0,0779) |
| **SPOT (new, spring)** | 0,2428 (±0,0699) | - | 0,2755 (±0,0822) |

#### 2.3.7.1. Mound parameters in Albany Thicket

The significance of differences in means of spatial data in the Albany Thicket could not be tested due to the small sample size (n = 6). High-density plots had a larger frequency percentage of Voronoi hexagons, number of polygon sides, and greater PCF peaks (*g*(*r*)) compared to low-density plots (Table 2.9). The latter, in turn, had greater mound diameters, nearest neighbour distances, R-dispersion coefficient values, and distances (*r*) of PCF peaks (Table 2.9).

**Table 2.9.** The mean (± standard deviation) spatial properties of *Microhodotermes viator* mounds from the Albany Thicket, including desnity, mound diameter, nearest neighbour distance, R-dispersion coefficient, percentage of hexagonal polygons in Voronoi tessellations and number of sides per polygon, greatest pair correlation function peaks *g*(*r*), and the corresponding distance of peaks (*r*).

| | **High-density** | **Low-density** |
|---|---|---|
| **Density (mounds/km$^2$)** | 408 (±284) | 189 (±94) |
| **Diameter (m)** | 21,59 (±4,62) | 32,11 (±4,23) |
| **Nearest neighbour distance (m)** | 41,47 (±11,85) | 45,42 (±5,80) |
| **R-dispersion coefficient** | 0,7602 (±0,6253) | 1,1180 (±0,1560) |
| **% Hexagons** | 38,46 (±2,73) | 32,11 (±4,23) |
| **Mean number of sides/polygon** | 5,83 (±0,04) | 5,79 (±0,14) |
| **PCF peak or g(r)** | 1,82 (±0,21) | 1,63 (±0,30) |
| **Peak distance (r)** | 53,90 (±13,97) | 62,51 (±30,80) |

There was no significant difference in any of the productivity values from the MODIS, SPOT (old and new) datasets between any combination of density (high and low) and habitat (mound or matrix) treatments of the respective datasets (Table 2.10). However, matrix habitats had higher autumn and spring MODIS and autumn SPOT (old) NDVI values than their associated mound habitats, and mounds had higher spring and autumn SPOT (new) values than their associated matrix habitats (Table 2.10).

**Table 2.10.** The mean (± standard deviation) productivity values from the MODIS and SPOT (old and new) datasets and their respective Tukey groupings in bold italics for the Albany Thicket.

| | **High-density** | | | | **Low-density** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Mound** | | **Matrix** | | **Mound** | | **Matrix** | |
| **MODIS (autumn)** | 0,309 (±0,080) | ***a*** | 0,320 (±0,072) | ***a*** | 0,365 (±0,102) | ***a*** | 0,372 (±0,102) | ***a*** |
| **MODIS (spring)** | 0,259 (±0,082) | ***b*** | 0,269 (±0,075) | ***b*** | 0,292 (±0,103) | ***b*** | 0,301 (±0,104) | ***b*** |
| **SPOT (old, autumn)** | 0,165 (±0,014) | ***c*** | 0,170 (±0,025) | ***c*** | 0,173 (±0,031) | ***c*** | 0,180 (±0,029) | ***c*** |
| **SPOT (new, autumn)** | 0,176 (±0,079) | ***d*** | 0,150 (±0,096) | ***d*** | 0,166 (±0,051) | ***d*** | 0,157 (±0,055) | ***d*** |
| **SPOT (new, spring)** | 0,246 (±0,069) | ***e*** | 0,204 (±0,102) | ***e*** | 0,286 (±0,018) | ***e*** | 0,253 (±0,068) | ***e*** |

### 2.3.7.2. Mound parameters in Fynbos

There were no significant differences (*p* > 0.05 Student T-test and Mann-Whitney U) in any spatial data estimators described below between high and low-density plots in the Fynbos (n = 16). High and low-density plots had similar R-dispersion coefficients while high density plots had a higher frequency of hexagons, number of sides in Voronoi polygons, pair function correlation *g*(*r*) peaks, and the distance of *g*(*r*) peaks (*r*) compared to low-density plots (Table 2.11). Low-density plots had a larger mean mound diameter and larger nearest neighbour distance than high-density plots (Table 2.11).

**Table 2.11.** The mean (± standard deviation) spatial properties of *Microhodotermes viator* mounds from the Fynbos, including desnity, mound diameter, nearest neighbour distance, R-dispersion coefficient, percentage of hexagonal polygons in Voronoi tessellations and number of sides per polygon, greatest pair correlation function peaks *g*(*r*), and the corresponding distance of peaks (*r*).

| | **High-density** | **Low-density** |
|---|---|---|
| **Density (mounds/km$^2$)** | 207 (±58) | 130 (±31) |
| **Diameter (m)** | 22.32 (±3.14) | 23.13 (±1.76) |
| **Nearest neighbour distance (m)** | 44.75 (±5.21) | 50.62 (±7.27) |
| **R-dispersion coefficient** | 0,9593 (±0,2451) | 0,9566 (±0,2732) |
| **% Hexagons** | 35,41 (±4,83) | 32,88 ±4.63) |
| **Mean number of sides/polygon** | 5.82 (±0.06) | 5.78 (±0.12) |
| **PCF peak or g(r)** | 3.39 (±3.22) | 2.99 (±2.10) |
| **Peak distance (r)** | 62.60 (±15.45) | 60.69 (±20.61) |

The low-resolution (MODIS) productivity (NDVI) values for both autumn and spring were greater in high- (autumn = 0.3457 ±0.0920; spring = 0.3747 ±0.1217) compared to low-density plots (autumn = 0.3203 ±0.1045; spring = 0.3404 ±0.1372), while low-density plots had a higher autumn high-resolution (SPOT – old) NDVI (0.1303 ±0.0328) than high-density plots (0.1238 ±0.0286). None of these differences, however, were significant. Matrix habitats had greater spring MODIS NDVI values compared to that of mound habitats in both high- and low-density treatments, however, the same was only true for autumn NDVI in high-density treatments compared to low-density treatments where mounds had the greater MODIS NDVI (Table 2.12). In high-density treatments the SPOT (old) autumn NDVI was greater in matrix habitats compared to low-density plots where it was greater in mound habitats (Table 2.12). Following two-way ANOVA, however, none of these differences were significant. New SPOT data were not available for sites in the Fynbos.

**Table 2.12.** The mean (± standard deviation) productivity values from the MODIS and SPOT (old) datasets and their respective Tukey groupings in bold italics for the Fynbos.

| | **High-density** | | | | **Low-density** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Mound** | | **Matrix** | | **Mound** | | **Matrix** | |
| **MODIS (autumn)** | 0,3428 (±0,0938) | ***a*** | 0,3487 (±0,0976) | ***a*** | 0,3207 (±0,1084) | ***a*** | 0,3199 (±0,1071) | ***a*** |
| **MODIS (spring)** | 0,3710 (±0,1244) | ***b*** | 0,3784 (±0,1287) | ***b*** | 0,3391 (±0,1397) | ***b*** | 0,3417 (±0,1431) | ***b*** |
| **SPOT (old, autumn)** | 0,1201 (±0,0337) | ***c*** | 0,1275 (±0,0246) | ***c*** | 0,1348 (±0,0406) | ***c*** | 0,1257 (±0,0243) | ***c*** |

No significant relationships were found between productivity (NDVI) and any of the measured spatial variables in high-density plot treatments. However, nearest neighbour distance had significant negative relationships with both autumn (cor = -0.71, $p < 0.01$) and spring (cor = -0.73, $p < 0.01$) MODIS NDVI.

### 2.3.7.3. Mound parameters in Succulent Karoo

Compared to low-density plots, high density plots had a larger mound diameter, R-dispersion coefficient, and frequency of hexagons (Table 2.13). The number of sides of Voronoi polygons was the same for high and low-density plots (Table 2.13). The mean nearest neighbour distance, pair function correlation $g(r)$ peaks, and the distance of $g(r)$ peaks ($r$) of lwo-density plots were greater than those of high-density plots (Table 2.13).

**Table 2.13.** The mean (± standard deviation) spatial properties of *Microhodotermes viator* mounds from the Succulent Karoo, including desnity, mound diameter, nearest neighbour distance, R-dispersion coefficient, percentage of hexagonal polygons in Voronoi tessellations and number of sides per polygon, greatest pair correlation function peaks $g(r)$, and the corresponding distance of peaks ($r$) ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Mann-Whitney U).

| | **High-density** | **Low-density** |
|---|---|---|
| **Density (mounds/km$^2$)** | 324 (±114)******* | 167 (±71)******* |
| **Diameter (m)** | 25,10 (±6,54) | 23,95 (±4,92) |
| **Nearest neighbour distance (m)** | 41,15 (±6,72)******* | 53,26 (±11,37)******* |
| **R-dispersion coefficient** | 1,1363 (±0,1219) | 1,0858 (±0,1639) |
| **% Hexagons** | 36,30 (±3,99) | 33,72 (±5,54) |
| **Mean number of sides/polygon** | 5,81 (±0,08) | 5,81 (±0,07) |
| **PCF peak or g(r)** | 1,89 (±0,38) | 2,00 (±0,70) |
| **Peak distance (r)** | 56,46 (±15,41) | 62,04 (±15,47) |

Productivity values (NDVI) of the Succulent Karoo from all available datasets are compared in Table 2.14. High-density plots had higher productivity (NDVI) in all datasets, except for the old high-resolution SPOT autumn dataset where low-density plots had a higher NDVI. Mounds had higher NDVI compared to matrix habitats in all datasets except the low-resolution MODIS and high-resolution SPOT (new) autumn datasets where the matrix had a higher mean NDVI (Table 2.14). Following two-way ANOVA, however, none of these differences were significant in the Succulent Karoo

**Table 2.14.** The mean (± standard deviation) productivity values from the MODIS and SPOT (old and new) datasets and their respective Tukey groupings in bold italics for the Succulent Karoo.

| | **High-density** | | | | **Low-density** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Mound** | | **Matrix** | | **Mound** | | **Matrix** | |
| **MODIS (autumn)** | 0,2331 (±0,0612) | ***a*** | 0,2333 (±0,0611) | ***a*** | 0,2225 (±0,0650) | ***a*** | 0,2234 (±0,0658) | ***a*** |
| **MODIS (spring)** | 0,2198 (±0,0709) | ***b*** | 0,2178 (±0,0696) | ***b*** | 0,2114 (±0,0727) | ***b*** | 0,2095 (0,0713) | ***b*** |
| **SPOT (old, autumn)** | 0,1194 (±0,0343) | ***c*** | 0,1252 (±0,0293) | ***c*** | 0,1334 (±0,0437) | ***c*** | 0,1221 (±0,0328) | ***c*** |
| **SPOT (new, autumn)** | 0,2001 (±0,0564) | ***d*** | 0,1899 (±0,0715) | ***d*** | 0,1897 (±0,0869) | ***d*** | 0,1895 (±0,0963) | ***d*** |
| **SPOT (new, spring)** | 0,2891 (±0,0660) | ***e*** | 0,2732 (±0,0833) | ***e*** | 0,2722 (±0,0880) | ***e*** | 0,2695 (0,0947) | ***e*** |

When high and low-density plots in the Succulent Karoo were grouped together the density of mounds had significant positive relationships with autumn (cor = 0.29, $p < 0.05$) and spring (cor = 0.28, $p < 0.05$) MODIS NDVI. Nearest neighbour distance had significant negative relationships with autumn (cor = -0.32, $p < 0.05$) and spring (cor = -0.32, $p < 0.05$) MODIS, and autumn SPOT (new) productivity (cor = -0.38, $p < 0.05$) when all plots were grouped together, but also with spring MODIS NDVI in low-density-only treatments (cor = -0.39, $p < 0.05$). The R-dispersion coefficients had no significant relationship with NDVI in high-density-only treatments, but had significantly negative relationships with both autumn (cor = -0.43, $p < 0.01$) and spring (cor = -0.40, $p < 0.01$) MODIS NDVI when plots were grouped together, and with both autumn (cor = -0.55, $p < 0.01$) and spring (cor = -0.53, $p < 0.01$) MODIS NDVI in low-density-only treatments.

### 2.3.8. Modelling the influence of rainfall and vegetative productivity on density of *M. viator* mounds

#### 2.3.8.1. Low-resolution MODIS productivity

The first group of models tested to explain the density of *M. viator* mounds using the low-resolution MODIS autumn productivity values (NDVI) of the matrix. In total 69.49 % of the variation in density of *M. viator* mounds was explained (SE = 75.45, df = 66, $p < 0.001$) by the overall (OMA1) model (Table 2.15). When removing the '*Biome*' factor from the model and testing the density of each biome separately, the sample size for the Albany Thicket biome was too small (n = 6) and residuals had zero degrees of freedom, so models could not be tested for the Albany Thicket. The Fynbos models, however, were not significant ($p >$ 0.05). However, the model of the Succulent Karoo biome (SKMA1) explained 77.98 % (SE = 62.96, df = 45, $p < 0.001$) of the mound density (Table 2.15). When autumn NDVI was substituted with spring NDVI values in the models above, the overall model for spring (OMS1) explained a greater (69.99 %) amount of the observed variation in mound density (SE = 74.79, df = 66, $p < 0.001$) than autumn NDVI (Table 2.15). Removing the '*Biome*' factor from the latter model and testing only the Succulent Karoo variables, the resulting model (SKMS1) explained 77.54 % (SE = 63.59, df = 45, $p < 0.001$) of the observed variation in density (Table 2.15).

**Table 2.15.** Coefficients for variables (nearest neighbour distance – NN; R-dispersion coefficient – Rcoef; frequency percentage of hexagons = Hex; Diameter; mean annual precipitation – MAP; autumn NDVI; biome; bioregion; and vegetation unit) in the equation using the MODIS productivity dataset to determine the observed density of *Microhodotermes viator* mounds for the models discussed above.

| Variable | OMA1 | SKMA1 | Variable | OMS1 | SKMS1 |
|---|---|---|---|---|---|
| **Intercept** | 540,09 | 425,01 | **Constant** | 558,70 | 451,07 |
| **NN** | -9,16 | -8,83 | **NN** | -9,35 | -8,95 |
| **Rcoef** | 35,26 | 180,11 | **Rcoef** | 21,91 | 157,66 |
| **Hex** | 4,15 | 1,73 | **Hex** | 4,25 | 2,06 |
| **Diameter** | 0,79 | -1,85 | **Diameter** | 1,38 | -1,62 |
| **MAP** | -0,08 | -0,02 | **MAP** | -0,07 | -0,03 |
| **Autumn NDVI** | -96,34 | 272,33 | **Spring NDVI** | -151,17 | 176,35 |
| **Biome** | -2,40 | - | **Biome** | -5,86 | - |
| **Bioregion** | -4,30 | -4,45 | **Bioregion** | -3,50 | -2,59 |
| **Veg unit** | 0,28 | 0,49 | **Veg unit** | 0,40 | -0,38 |

The influence of rainfall (MAP) and productivity (NDVI) on density was compared by removing each of these variables from the models above and estimating the amount of variance explained in the presence of one, and absence of the other. Overall autumn (OMA1) and spring (OSA1) models both explained 70 % of the observed variation in *M. viator* mound density. Omitting productivity (NDVI) from either model explained 69 % of this variation, which was equal to the amount of variation explained by omitting rainfall (MAP) from the spring model, but higher than omitting MAP from the autumn model (68 %). In the Succulent Karoo, both autumn (SKMA1) and spring (SKMS1) models explained 78 % of the variation in mound density. This was equal to the amount explained by omitting MAP from either model but higher than omitting NDVI (77 %). A summary of models is presented in Appendix E.

#### 2.3.8.2. High-resolution SPOT productivity

Replacing the low-resolution (MODIS) autumn productivity in model OMA1 with high-resolution (SPOT) autumn productivity (NDVI) of the matrix from an old dataset, the new model (OSA1) explained 70.29 % (SE = 74.32, df = 66, $p < 0.001$) of the observed variation in *M. viator* mound density (Table 2.16). As in the previous section, the '*Biome*' factor was removed from the model and the density of each biome was tested separately. The sample size (n = 6) and resulting residual degrees of freedom of the Albany Thicket was too low for model testing. Using these high-resolution autumn SPOT data from an older dataset in the overall Fynbos model did not result in a significant model to predict the density of *M. viator* mounds ($p$ = 0.1910). However, using these data in the overall model for the Succulent Karoo (SKSA1) explained 78.28 % (SE = 62.54, df = 45, $p < 0.001$) of the observed variance of mound density (Table 2.16).

**Table 2.16.** Coefficients for variables (nearest neighbour distance – NN; R-dispersion coefficient – Rcoef; frequency percentage of hexagons = Hex; Diameter; mean annual precipitation – MAP; autumn NDVI; biome; bioregion; and vegetation unit) in the equation using the autumn SPOT (old and new) productivity datasets to determine the observed density of *Microhodotermes viator* mounds for the models discussed above.

| Variable | OSA1 | SKSA1 | OSA2 | SKSA2 |
|---|---|---|---|---|
| **Intercept** | 602,54 | 550,73 | 779,63 | 813,51 |
| **NN** | -8,97 | -9,13 | -8,81 | -8,10 |
| **Rcoef** | 52,60 | 116,29 | -118,21 | 22,12 |
| **Hex** | 4,23 | 3,39 | 5,81 | 3,94 |
| **Diameter** | -0,67 | -1,57 | 2,89 | -0,39 |
| **MAP** | -0,09 | -0,03 | -0,51 | -0,37 |
| **Autumn NDVI** | -502,65 | -476,10 | -1016,04 | -620,21 |
| **Biome** | -4,46 | - | 64,25 | - |
| **Bioregion** | -5,48 | -2,05 | -39,45 | -35,08 |
| **Veg unit** | 0,23 | -0,37 | 2,68 | -1,97 |

Replacing the old autumn SPOT values in model OSA1 with the corresponding new autumn SPOT values to produce model OSA2 explained 79.07 % (SE = 80.36, df = 24, $p < 0.001$) of the observed variance in mound density (Table 2.16). The sample size of Fynbos (n = 0) and Albany Thicket (n = 6) was too low in the new autumn SPOT dataset, in addition, the residual degrees of freedom was too low in Albany Thicket to test the model predicting the density of *M. viator* mounds. New autumn SPOT NDVI, however, explained 79.65 % (SE = 71.31, df = 19, $p < 0.001$) of the observed variance in mound densities in the Succulent Karoo (Table 2.16).

The final dataset replaces the new high-resolution autumn SPOT with new high-resolution spring SPOT data. Making this replacement in model OSA2 produced the model OSS1 which explained 76.05 % (SE = 85.73, df = 23, $p < 0.001$) of the observed variance in mound density (Table 2.17). Replacing the new high-resolution autumn SPOT data with new high-resolution spring SPOT data could not test models for the Albany Thicket or Fynbos biomes, as mentioned above. However, testing the Succulent Karoo model SKSS1 using the new spring data was able to explain 75.65 % (SE = 74.92, df = 19, $p < 0.001$) of the observed variation in mound density (Table 2.17).

**Table 2.17.** Coefficients for variables (nearest neighbour distance – NN; R-dispersion coefficient – Rcoef; frequency percentage of hexagons = Hex; Diameter; mean annual precipitation – MAP;  autumn NDVI; biome; bioregion; and vegetation unit) in the equation using the spring SPOT (old and new) productivity datasets to determine the observed density of *Microhodotermes viator* mounds for the models discussed above.

| Variable | OSS1 | SKS1 |
|---|---|---|
| **Intercept** | 699,88 | 506,32 |
| **NN** | -8,23 | -7,57 |
| **Rcoef** | -104,24 | 27,97 |
| **Hex** | 7,31 | 4,95 |
| **Diameter** | 4,86 | -0,96 |
| **MAP** | -0,44 | -0,25 |
| **Spring NDVI** | -654,49 | -76,39 |
| **Biome** | -17,86 | - |
| **Bioregion** | -12,92 | -11,45 |
| **Veg unit** | 3,52 | -2,73 |

As in the previous section the influence of rainfall (MAP) and productivity (NDVI) on density were compared by removing each of these variables from the models above and estimating the amount of variance explained in the presence of one, and absence of the other.

Omitting either MAP or NDVI from the model using old, autumn SPOT data (OSA1) both explained 69 % of the observed variation in *M. viator* density, compared to 70 % in the complete model. In the Succulent Karoo model (SKSA1) using the same dataset, however, removing NDVI from the model explained 77 % compared to 79 % when instead MAP is removed.

Omitting NDVI from the model using new SPOT data for autumn (OSA2) explained 71 % of the variation in *M. viator* mound density, compared to 76 % if instead MAP is omitted. Using this same dataset for the Succulent Karoo model (SKSA2) omitting NDVI explained 77 %, compared to 78 % if instead MAP was omitted.

Omitting MAP from the new SPOT data for spring the model (OSS1) explained 73 % of the observed variation in *M. viator* mound density, compared to 71 % if instead NDVI is omitted. In the Succulent Karoo, however, the model using this spring data that best explained the density of mounds was the model omitting NDVI (77 %) compared to the total model (76 %) or omitting MAP instead (75 %).

## 2.4. Discussion

### 2.4.1. Factors influencing mound density and size

Almost all previous work on *M. viator* mounds has investigated high density sites. High-density plots in this study had 309 mounds/km$^2$, compared to values of 250 mounds/km$^2$ in Prince Albert (Milton *et al.*, 1992), 300 mounds/km$^2$ (Cramer and Midgley, 2015) and 297 mounds/km$^2$ (Picker *et al.*, 2007) from satellite images across the distribution range of sand-capped mounds of *M. viator.* Higher densities have been reported from the Succulent Karoo of 450 mounds/km$^2$ in Soebatsfontein, 500 mounds/km$^2$ across Namaqualand, 440 mounds/km$^2$ in Inverdoorn, and 380 mounds/km$^2$ in Laingsburg (McAuliffe *et al.*, 2014)

Overall no relationship was detected between mound density and rainfall, or density and any of the productivity (NDVI) datasets. Picker *et al*. (2007) similarly found no relationship between density and productivity, however, when values for sites in the Succulent Karoo alone were regressed against productivity a positive relationship was found. Similarly in this study, a positive relationship was found between mound density and productivity (both autumn and spring), but only with low-resolution (MODIS) datasets and not with high-resolution (SPOT) datasets.

The mean diameter of *M. viator* mounds in high-density plots was 24 m which is comparable with diameters determined in former studies; 13 m (Milton *et al.*, 1992), 16 m (McAuliffe *et al.*, 2018a), 17 m (Moore and Picker, 1991), and 32 m (Cramer and Barger, 2014). Regression analyses with new high-resolution (SPOT) datasets suggest a positive relationship between mound diameter and NDVI, with variation in other biotic and abiotic factors accounting for variation. Mound sizes were measured from Google Earth Pro (7.1.7.2606) and real size may vary depending on the resolution of the imagery. In addition, vegetation density at some sites may have obscured mounds and/or boundaries of mounds making size detection difficult to detect accurately.

Estimates of nearest neighbour distance include 50 m (Laurie, 2002; McAuliffe *et al.*, 2018a), 45 m (Juergens *et al.*, 2015), and 47 m (Lovegrove and Siegfried, 1989), compared to 42 m at high-density sites found in this study. Variation in the nearest neighbour distance is a function of resources and competitive interaction between colonies (Coaton, 1958; Laurie, 2002), and sand accretion may vary from site to site due to differences in sediment supply and wind (McAuliffe *et al.*, 2019). Negative relationships were detected between nearest neighbour distance and low-resolution (MODIS) autumn and spring productivity, consistent with the central foraging mechanism proposed by Laurie (2002) that increasing productivity will allow smaller foraging ranges and higher density of colonies (Picker *et al.*, 2007; Kunz *et al.*, 2012).

All pair correlation functions plotted with 95 % envelopes of random distribution had maximum peaks beyond this envelope indicating over-dispersion consistent with Juergens *et al*. (2015). In addition, the mean R-dispersion in high-density sites (1.07) was less than that reported by Juergens *et al*. (2015) and Cramer and Midgley (2015), viz. 1.56 and 1.27 respectively. However, when R-dispersion was determined for each biome, only the Succulent Karoo demonstrated over-dispersion (1.12) while the Albany Thicket (0.94) and Fynbos (0.96) values indicated under-dispersed patterns (Clark and Evans, 1954). Over-dispersion is associated with hexagonal patterns (Clark and Evans, 1954), and thus two-dimensional polygons of Voronoi tessellations are expected to have a mean of six sides, as has been determined for several cases of social-insect over-dispersion (Adams and Tschinkel, 1995; Juergens *et al.*, 2015). This study found hexagon frequencies of > 34 %. in all vegetation types.

### 2.4.2. Spatial patterns of high and low-density *M. viator* plots

Although the difference in NDVI between high and low-density plots was not significant, both the autumn and spring NDVI were higher in low-density plots compared to high-density plots, possibly reflecting greater (termite) herbivory in high density plots. Contiguous plots of high and low densities probably result from local environmental factors that affect soil and/or vegetation type which influence the establishment and success of *M. viator* colonies e.g. shallow soils would not be suitable for *M. viator* whose nest system is largely subterranean. Superficial nests on shallow soils would be exposed to aardvark predation - a major threat to the establishment and survival of *M viator* colonies (Moore and Picker, 1991), possibly explaining why productive sites should have low densities of mounds. Density may have been driven by local topography and soil type, as has been found in other species (Meyer *et al.*, 1999). In addition, the improved productivity generated by *M. viator* on mounds further complicates the interpretation of causation (Jones *et al.*, 1994; McAuliffe *et al.*, 2019). As logic dictates, a greater nearest neighbour distance was found in low-density plots compared to high-density plots. The fact that a higher percentage of hexagonal Voronoi tessellations occurred in high-density plots compared to low-density plots suggests more optimal packing of mounds in high density sites–into a restricted area (Laurie, 2002; Tarnita *et al.*, 2017).

The three biomes considered had similar mean NN, percentage of hexagonal Voronoi polygons, number of sides of Voronoi polygons, and distance of PCF peaks (*r*). The lowest mean density of mounds was found in the Fynbos biome and the highest in the Albany Thicket biome. The latter result was surprising, as the distribution of *M. viator* is centred in the Succulent Karoo biome (Coaton and Sheasby, 1974), which had the greatest R-dispersion values in this study. The second highest R-dispersion value was found in the Fynbos (0.96) biome and the lowest in the Albany Thicket biome (0.94).

The outcomes of comparative multifactorial models could not identify either rainfall or matrix productivity as a clear driver of *M. viator* mound density. In addition, the positive relationship of *M. viator* mound density with both autumn and spring productivity in the Succulent Karoo biome, and the lack of relationship identified in the Fynbos biome typically characterised by nutrient-poor soils, support the findings of Picker *et al*. (2007) that mound density is determined by productivity, which in turn is influenced by vegetation type and soil nutrient status. However, no relationship was found between MAP and any of the spatial variables (density, NN, or R-dispersion) in the Succulent Karoo biome. Nearest neighbour distance (NN) in both the Fynbos and Succulent Karoo biomes had negative relationships with both autumn and spring NDVI, in agreement with the density relationship described above nearest neighbour densities in both biomes decrease with increasing NDVI, which correlates with the optimal foraging theory of Laurie (2002).

According to Laurie (2002), over-dispersion is driven by territorial intra-specific competition based on resource availability. However, it has been noted that *M. viator* show a preference for clay soils, which explains their predominant distribution in the Succulent Karoo, compared with sandy soils associated with the Fynbos vegetation type (not renosterveld) of the Fynbos biome (Picker *et al.*, 2004; Mucina and Rutherford, 2006; Cramer *et al.*, 2017).

## 2.5. Conclusion

The bush-clump hypothesis for the genesis of heuweltjies (Cramer *et al.*, 2012) suggests that over-dispersion is the result of plant-soil feedback between facilitative and competitive interactions. Such mechanisms for pattern formation have been found elsewhere (Rietkerk and Van de Koppel, 2008; Jürgens *et al.*, 2020), however, has not been effectively demonstrated in the case of heuweltjies. One of the arguments against the termite theory was that *M. viator* colonies could not produce the degree of over-dispersion found in heuweltjies (Cramer and Midgley, 2015), however, McAuliffe *et al*. (2018a) was able to demonstrate similar over-dispersion patterns for different manifestations of *M. viator* colonies similar to that of other termite species and what was determined in this study. The findings of this chapter support the concept of optimal transport in central foraging for *M. viator* as proposed by Laurie (2002), having demonstrated a positive relationship between hexagonal patterning and density of *M. viator* mounds/heuweltjies in the Succulent Karoo. It is worth noting that this relationship was only found in the vegetation type where heuweltjie predominantly occur and not in the Fynbos where they are not as common.

# CHAPTER 3 – SOIL ENRICHMENT BY *MICROHODOTERMES VIATOR*

## 3.1. Introduction

Termites are considered allogenic ecosystem engineers because they are able to shape community structure and distributions. This is accomplished by influencing resource availability by modifying the physical and chemical properties of soil (Dangerfield *et al.*, 1998). A recent review describes the cascading effects of termites in savannas (Muvengwi and Witkowski, 2020). The authors describe how termitaria act as sources of enrichment in the landscape, promoting vegetation heterogeneity and generate denser patches that attract other animals as refugia or high-quality forage. The urine and dung of attracted mammals, and the activity of detritivores, contribute to this localized enrichment, creating a positive feedback loop. In the case of the southern harvester termite (*Microhodotermes viator*) McAuliffe *et al*. (2019) postulated a mechanism of several state changes resulting in the genesis of heuweltjies, the most obvious surface manifestation of the mounds of *M. viator*. (Chapter 1). The first transition is the establishment and persistence of a colony. This chapter explores how *M. viator* generates the second transition or primary state change of soils and heuweltjie genesis. These changes then, in turn, affect plant and animal community distribution and composition (Milton and Dean, 1990) (explored in Chapter 5).

### 3.1.1. Physical alteration of soils by termites

Physical changes in soil brought about by termites include increasing 1) the proportion of fine soil particles by selecting soils of particular particle size for mound construction (Jouquet *et al.*, 2002), 2) the formation of aggregates, tunnels and cemented walls (Lee and Wood, 1971b; Fall *et al.*, 2001; Brossard *et al.*, 2007; Abe *et al.*, 2009; Bonachela *et al.*, 2015), and 3) species-dependent changes in bulk density (Lee and Wood, 1971b; Abe *et al.*, 2009). Termites in general utilize fine (clay and silt), rather than coarse (sandy) soils, preferentially mixed with saliva for the construction of mounds and associated structures (Lee and Wood, 1971a; Mora *et al.*, 2003). Particle size, however, is limited to the maximum particle size workers can carry. A small portion of fine gravel (1 - 3 %) has been reported in mounds of species with comparatively large workers (*Drepanotermes rubriceps*, *Nasutitermes longipennis*, *N. magnus* and *N. triodiae*), compared to mounds of species with smaller workers (*Amitermes* spp., *Coptotermes acinaciformis*, *C. laeteus*, *Mastotermes darwiniensis*, *Microcerotermes nervosus* and *Schedorhinotermes actuosus*) where no gravel was detected (Lee and Wood, 1971a). The consequential increased porosity of nest soils (finer clay soils used in nest construction, and building of tunnels) improves soil-water properties (Lee and

Wood, 1971b; Lamoureux and O'Kane, 2012; Jouquet *et al.*, 2016; Apori *et al.*, 2020). Soils in Thailand inhabited by *Macrotermes* spp. had enhanced porosity, effectively improving the available water to plants when compared with the controls (Suzuki *et al.*, 2007). The introduction of termites (*Odontotermes* spp.) to crusted soils in Burkina Faso significantly improved water infiltration rates (Mando *et al.*, 1996). Water is essential for releasing soil nutrients to plants (Caldwell *et al.*, 1998; Carnol and Ineson, 1999) and consequently, in arid regions, the combined effect of termite-driven increases in water infiltration and nutrients can have localised effects on productivity and community processes.

### 3.1.2. Chemical alteration of soils by termites

Chemical modification of soil by termites is the result of redistribution of soils (Sarcinelli *et al.*, 2009), decomposition of dead termites (Dangerfield *et al.*, 1998), and decomposition of both food and faecal waste (Lee and Wood, 1971b; De Bruyn and Conacher, 1995; Brossard *et al.*, 2007). In addition to transporting soil particles from deeper soil horizons to the surface (representing an enrichment of mineral nutrients and exchangeable cations), termites often cement faecal pellets (frass) into mound structures (Jouquet *et al*. 2005; 2011). The origin of transported particles used in construction can influence soil chemistry in different ways (Cheik *et al.*, 2019) e.g. humivores that use nutrient-rich faeces, or fungus-feeding termites which use soil material mixed with saliva and limited amounts of faeces (Fall *et al.*, 2001; Jouquet *et al.*, 2011) maintain significantly higher nutrient concentrations compared to the associated matrix soils (Muvengwi and Witkowski, 2020). The average termite body nitrogen content for several termite species and their castes ranges between 5.6 – 12.6 % dry mass (Matsumoto, 1976). This and other minerals are temporarily immobilized within the bodies of termites, but released back into the nutrient cycle when termites die. The bulk of termites' influence on the chemical properties of soil is, however, derived from the decomposition of centrally stored food which is gathered from a larger peripheral area, and frass (Abe *et al.*, 2011).

### 3.1.3. Termite soil enrichment

Much work has been done on the soil nutrient concentrations of nests of different termite species, as summarized in Table 3.1. Nest soils of termite species tend to have a more basic pH than that of matrix soils, with the exception of *Cubitermes niokoloensis* and *Macrotermes subhyalinus*. This is attributed to the accumulation of calcium carbonate associated with termite nests (Lee and Wood, 1971b). The mean enrichment ratios of nest soils for different termite species indicate that nest soils are enriched for most elements and nutrients

(Table 3.1). Exceptions include relative enrichment of P by *M. bellicosus* and *M. falciger* nest soils, and enrichment of C and N in *Gnathamitermes perplexus* nest soils, which were lower than that of matrix soils. Nest soils of *M. viator* in the Worcester-Robertson valley, close to the study site of this dissertation, were found to be enriched with Al, B, Ca, Cu , Fe, K, Mg, Mn, N, Na, P and Zn  relative to the surrounding matrix soils (Midgley and Musil, 1990).

### 3.1.4. Objectives

The hypotheses that heuweltjies (as defined by McAuliffe *et al*. 2019) are the product of differential erosion (Cramer *et al.*, 2012) or aeolian sediment deposition (Cramer and Barger, 2014; McAuliffe *et al.*, 2014) as the result of dense plant roots keeping the soil intact, and dense plant canopies that trap and protect windblown soil by bush clumps respectively, are further tested by examining the nutrient profile of *M. viator* frass. If bush clumps alone are hypothesized to be the source of nutrient enrichment of heuweltjies, then the nutrient levels observed need to be commensurate with those of decomposed plant material. Alternatively, if the nutrient profile of heuweltjies more closely matches that of *M. viator* frass, then this might provide support for a termite origin of heuweltjies. Cramer & Barger (2014) cite Schlesinger *et al*. (1990) who stated that soil resources can be further localized beneath canopies of desert shrubs, to support a role of trees and shrubs on local soil resources to support their theory of the bush-clump origin of heuweltjies. Schlesinger *et al*. (1990), however, also acknowledged the existence of pre-existing soil heterogeneity for the establishment of desert bush-clumps. This chapter will compare the soil enrichment of *M. viator* with that of various sources of bush-clumping enrichment (Schlesinger *et al.*, 1996; Jarvel and O'Connor, 1999; Escudero *et al.*, 2004; Abanda *et al.*, 2011).

*M. viator* produces very large earth mounds, on top of which occur extensive piles of frass deposited by the colony. This frass is generated within the large hive and deposited above it (Moore and Picker, 1991). This behaviour is unique amongst termites, allowing for direct analysis of both the quantity and nutrient composition of termite frass. In other termite species, the frass is either dispersed or incorporated into the mound walls (Jouquet *et al.*, 2011), making the analysis of its composition difficult, and necessitating analysis of mound

**Table 3.1.** Nutrient concentrations and pH ratios (to account for different units of measurement from the different references) of several termite species' nest soils compared to matrix soils.

| Species | Ratio | B | C | Ca | Cu | Fe | K | Mg | Mn |
|---|---|---|---|---|---|---|---|---|---|
| *Cubitermes niokoloensis* [4] | matrix:nest | | 1:4,04 | | | | | | |
| *Gnathamitermes perplexus* [1] | matrix:nest | | 1:1,43 | 1:2,35 | | | 1:1,24 | 1:1,89 | |
| *Heterotermes aureus* [1] | matrix:nest | | 1:2,43 | 1:4,19 | | | 1:2,77 | 1:3,78 | |
| *Macrotermes bellicosus* [5] | matrix:nest | | 1:1,09 | 1:2 | | | 1:28,33 | 1:5,07 | |
| *Macrotermes falciger* [8] | matrix:nest | 1:5,32 | | 1:9,42 | 1:2,62 | 1:1,6 | 1:3,62 | 1:4,5 | 1:1,9 |
| *Macrotermes subhyalinus* [7] | matrix:nest | | | 1:1,02 | | | '1:3,02 | 1:0,89 | |
| *Microhodotermes viator* [2,6] | matrix:nest | 1:3,72 | 1:2,05 | 1:13,13 | 1:2,4 | 1:1,97 | 1:3,44 | 1:5,11 | 1:5,21 |
| *Nasutitermes ephratae* [3] | matrix:nest | | 1:3,79 | | | | | | |
| Mean (±sd) | matrix:nest | 1:4,52 (±1,13) | 1:2,68 (±1,21) | 1:5,95 (±4,85) | 1:2,51 (±0,16) | 1:1,79 (±0,26) | 1:8,24 (±10,45) | 1:3,87 (±1,76) | 1:3,56 (±2,34) |

| Species | Ratio | N | Na | $NH_4$ | $NO_3$ | P | Zn | pH |
|---|---|---|---|---|---|---|---|---|
| *Cubitermes niokoloensis* [4] | matrix:nest | 1:5,25 | | 1:83,41 | 1:42,07 | | | 6,1:5,1 |
| *Gnathamitermes perplexus* [1] | matrix:nest | 1:0,10 | 1:4,12 | 1:1 | 1:1,31 | | | 6,8:7,6 |
| *Heterotermes aureus* [1] | matrix:nest | 1:1,43 | 1:5,94 | 1:11 | 1:0,68 | | | 6,8:7,9 |
| *Macrotermes bellicosus* [5] | matrix:nest | 1:1,74 | 1:2 | | | 1:0,53 | | 6,6:7 |
| *Macrotermes falciger* [8] | matrix:nest | | 1:19,2 | 1:1,12 | 1:52,96 | 1:0,62 | 1,47 | 5,3:7,6 |
| *Macrotermes subhyalinus* [7] | matrix:nest | 1:1,89 | 1:2,74 | | | | | 9,1:8,2 |
| *Microhodotermes viator* [2,6] | matrix:nest | 1:1,79 | 1:1,06 | | | 1:9,26 | 1:4,56 | 4,4:7,1 |
| *Nasutitermes ephratae* [3] | matrix:nest | 1:3,51 | | 1:50,75 | 1:0,83 | 1:2,25 | | 4,8:5,6 |
| Mean (±sd) | matrix:nest | 1:2,62 (±1,66) | 1:6,19 (±6,76) | 1:36,57 (±36,57) | 1:24,14 (±25,80) | 1:3,17 (±4,14) | 1:3,02 (±2,19) | 6 (±2):7 (±1) |

(Nutting *et al*. 1987[1]; Midgley & Musil, 1990[2]; Lopéz-Hernández, 2001[3]; Ndiaye *et al*., 2004[4]; Abe *et al*., 2011[5]; Kunz *et al*., 2012[6]; Tilahun *et al*., 2012[7]; Seymour *et al*., 2014[8]) soils as a proxy for the frass itself. In this chapter, the mechanism of soil nutrient enrichment by *M. viator* is examined by exploring the amount of frass production, the rate of nutrient leaching from frass into the soil, and quantifying the nutrient profile of *M. viator* frass and nest soils compared to that of other termite species and their associated matrix soils. The amount of frass production and rate of leaching represent novel measurements to describe the magnitude of impact by *M. viator* on the local landscape, and describe the variation in nutrient profiles associated with *M. viator* nests across nine sites along a rainfall gradient from mesic to arid. The mean soil nutrient profile established in this way can be compared to previously determined soil nutrient profiles associated with *M. viator* as well as other termite species.

## 3.2. Materials and methods

### 3.2.1. Site selection and description

A single site (Worcester) was used for the quantification of frass and to examine nutrient leaching from frass. This site provided a unique opportunity since shallow soils on bedrock in this area forced *M. viator* colonies to locate nests superficially. As a result, the bulk of nest frass was deposited in substantial piles that represent cumulative depositions over an unknown length of time. This unusual situation enabled the quantification of frass load per nest, but also served as a source of pure frass for use in leaching experiments. Nine mature, medium size (diameter 14.7 – 23.0 m, mean 20.2 ± 3.2 m) *M. viator* nests (Figure 3.1.a) were randomly selected to quantify the amount of superficial frass present.

Nine additional sites identified from satellite images (Chapter 2) were selected for an analysis of the degree of enrichment in nest and matrix soil types (Figure 3.1.b). Sites were selected according to a rainfall gradient (See Appendix A). More mesic sites, with a mean annual precipitation (MAP) > 250 mm, were located in the Fynbos biome (Malmesbury, Koringberg, Tulbagh and Stellenbosch) (SAWS, 2018). Arid sites (MAP < 250 mm) were mostly in the Succulent Karoo biome (Prince Albert, Vanrhynsdorp and Calitzdorp) but included one site in the Fynbos biome (Clanwilliam) and one in the Albany Thicket biome (Oudtshoorn) (Mucina and Rutherford, 2006).

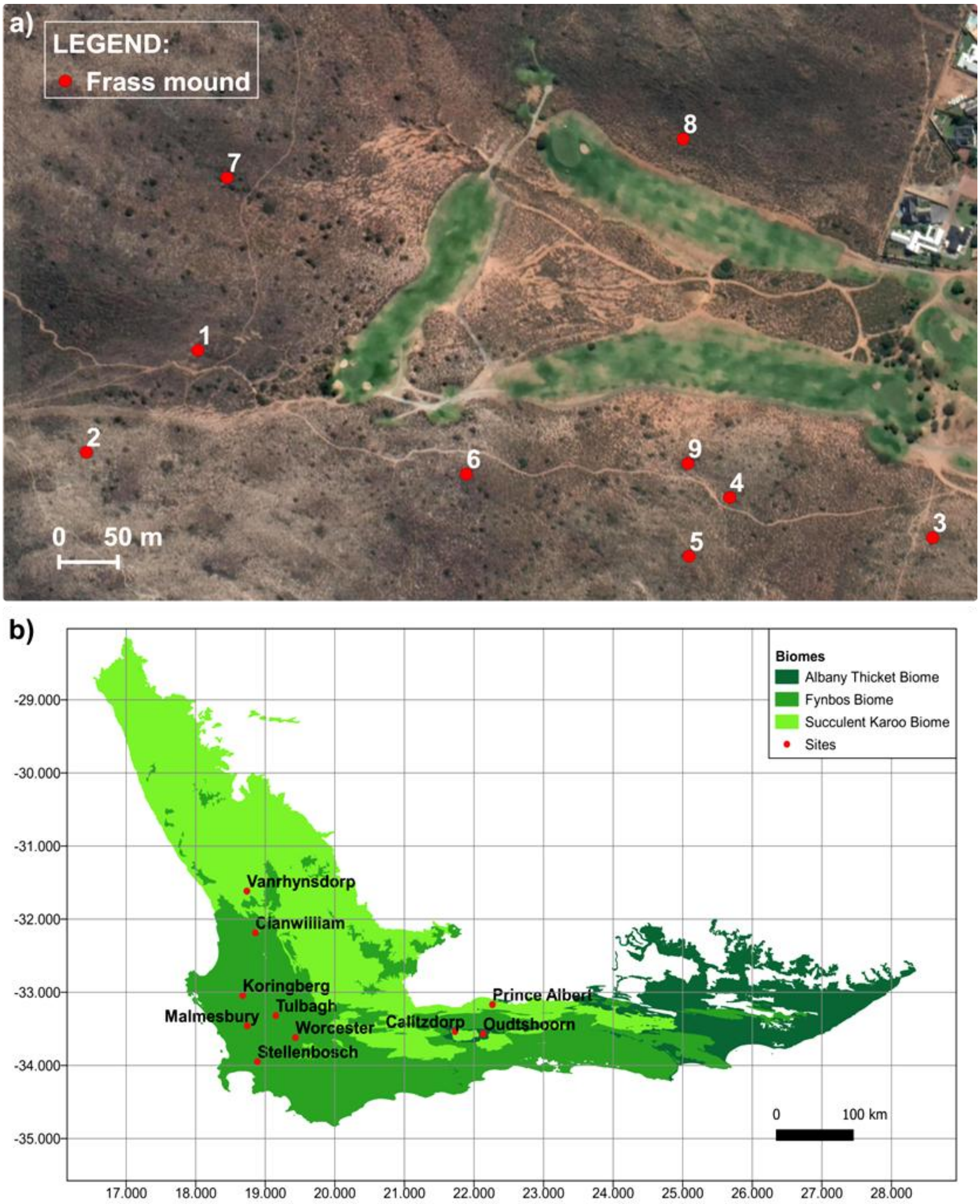

**Figure 3.2.a)** Mounds used for frass quantification in Van Riebeeck Park, Worcester (QGIS Google Satellite Openlayers Plugin, 31/12/2016). The green belt is an irrigated golf course, **b)** sites of nest and matrix soil collection for nutrient (C, Ca and N) analysis and comparison in the Albany Thicket, Fynbos and Succulent Karoo biomes of the Western Cape.

### 3.2.2. Frass quantification at Worcester

Piles of pure frass pellets (almost black when fresh, turning greyish or even white when dry and older) deposited by the termites on top of the nest surface were excavated (March 2017) from nine medium-sized (14.7 – 23 m diameter) *M. viator* nests at the study site to estimate the mass of deposited frass. These extensive and superficial frass piles covered up to 20% of the surface of some nests and were formed from the deposition of pure frass from a few exit tunnels subtending the subterranean hive. Once a frass pile develops, fresh frass is deposited on the top via constant elongation of tunnels subtending the hive. These frass 'dumps' are free of soil, which is deposited some distance from the nest through other (foraging) tunnel systems that radiate from the nest (Moore and Picker, 1991). The piles were carefully transferred with a spade into a 25 L bucket that was emptied some distance away into the matrix. The total number of buckets collected on each nest was recorded, and an average weight per bucket (8.99 ±2.59 kg), calculated from the mean weight derived from 21 randomly-sampled buckets of frass, was determined. The mass of frass present on each of the nine nest systems was then calculated. The lowest levels of the frass dumps, which were in contact with the soil, were left *in situ* to avoid contaminating the collected frass with soil.

### 3.2.3. Comparing nutrient profiles of nest and matrix soils

The *M. viator* nest and matrix plots used for sampling nutrient profiles of nest and matrix soils at Worcester were not the same as those that were used for frass quantification. At each plot 10 soil samples (± 1 kg, mixture of 10 random sub-samples) of the upper soil layer + depth of 10 – 15 cm were collected (October – November 2017) from each plot (the 10x mounds and 10x matrix). Each of the 200 soil samples was crushed and passed through a 2 mm sieve to remove stones and debris, and air-dried for 48 h in preparation for nutrient analysis. Nutrients measured were carbon (C), calcium (Ca) and nitrogen (N), as these are consistently higher in the nest than matrix habitats for several termite species (Table 3.1) and important for plant growth (Dangerfield *et al.*, 1998; Nabors, 2004). A 50 g sub-sample of each prepared sample was analysed at the Diagnostics Laboratory of the Department of Agriculture, Elsenburg (Stellenbosch) using the following methods:

The C content (%) of sub-samples was determined using the Walkley-Black method (Walkley and Black, 1934) as described in the Handbook of Standard Soil Testing Methods for Advisory Purposes (SSCSA, 1990). Organic material was oxidized by treatment with a warm $K_2Cr_2O_7$ and sulphuric acid mixture. The excess dichromate was then titrated with iron (II) ammonium sulphate hexahydrate and, assuming a valence of zero for soil organic matter, the reduced dichromate was considered equal to the amount of carbon present in the sample.

Soluble Ca was derived from the soil sample using a 1% citric acid solution which displaces exchangeable cations and prevents re-adsorption by forming citric acid complexes (Dyer, 1894; SSCSA, 1990). The product was then analysed using an Inductively Coupled Plasma Spectrometer to determine the concentration (cmol.mol$^{-1}$) of calcium in the soil sample.

Nitrogen content (%) was determined using the Kjeldahl method (Bremner, 1960). A weighed soil sample was digested using sulphuric acid to produce ammonium sulphate which was then converted into ammonia gas with the addition of an alkali. The ammonia gas was then distilled into a measured volume of standardized acid (commonly HCl or $H_2SO_4$) to become an ammonium solution and the nitrogen content determined through titration (SSCSA, 1990).

Log-transformed data were used to plot the Non-metric Multi-Dimensional Scaling of nutrient profiles for each site and habitat using the Plymouth Routines in Multivariate Ecological Research (PRIMER) software. The data did not meet the assumption of normality to perform Multivariate Analysis of Variance (MANOVA), therefore the variation in the site and habitat nutrient profiles was examined using the two-factor, non-parametric, permutation-based analogue between multiple groups based on distance measures, Permutational MANOVA (PERMANOVA) (Anderson, 2001; Anderson and Walsh, 2013). The PERMANOVA were carried out using 9999 permutations of the standardized raw data and Euclidean distance, and related *post hoc* tests were conducted in R Statistic Software (version 3.6.1) using the *vegan* (Oksanen *et al.*, 2007) and *pairwiseAdonis* (Arbizu, 2019) packages. Finally, the nutrient profiles determined for *M. viator* nests (heuweltjies) in this study were combined with that of others from literature and compared to nutrient profiles of bush-clumps and mounds of other termite species.

### 3.2.4. Frass decomposition and leaching of nutrients from frass

Pure frass was collected from the nine *M. viator* nests used for frass nutrient quantification (March 2017) in Worcester, mixed, and replicates of 1.5 kg placed in each of 20 frass packs (pouches prepared from green shade cloth 25 x 25 cm, with mesh openings of 1 mm$^2$). After taking a soil sample (± 500 g from the surface to 5 cm depth) where each frass pack would be randomly positioned in the matrix in Worcester, the packs were secured in position in the matrix with identifying metal pegs at each corner of the pack, and its location recorded using a Garmin eTrex 10 GPS. Paired samples of frass (from each pack) and soil (from each area where packs were placed) were prepared as above at the onset of the decomposition trial and delivered to the Diagnostics Laboratory of the Department of Agriculture, Elsenburg (Stellenbosch) to establish baseline measurements of C, Ca and N concentrations.

After 15 months had elapsed (October 2017 – January 2019), with a total rainfall of 309 mm recorded during this period, 18 of the 20 packs were retrieved (the remaining two were lost to human or wildlife interference). A small soil sample (± 500 g from the surface to 5 cm depth) was collected beneath each pack upon termination of the experiment. These soil samples, along with frass from the retrieved frass pack above the soil were prepared (as above) and delivered to the Diagnostics Laboratory of the Department of Agriculture, Elsenburg (Stellenbosch) to determine C, Ca and N concentrations upon termination of the experiment.

## 3.3. Results

Regressions between rainfall (MAP) and nutrient concentrations determined there was no clear pattern or relationship between MAP and either carbon (C), calcium (Ca) or nitrogen (N) concentrations in the matrix ($p = 0.6156$, $p = 0.5270$, $p = 0.7537$, respectively) or nest habitats ($p = 0.4146$, $p = 0.9320$, $p = 0.6610$, respectively). The total mean concentrations of C, Ca and N were higher in arid (MAP 143-245 mm) than mesic (MAP 286-1061 mm) sites, however, none of these differences were significant (Table 3.2). Nest habitats in both arid and mesic sites had greater mean concentrations of all measured nutrients, however, only the differences in C concentration in arid sites and N concentration in mesic sites were significant (Table 3.2).

**Table 3.2.** The mean (± standard deviation) concentrations of carbon, calcium and nitrogen in arid (MAP 143-245 mm) and mesic (286-1061 mm), and their respective matrix and *Microhodotermes viator* nest habitats ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Student T-test).

| | **Arid** | **Mesic** | **Nest (arid)** | **Matrix (arid)** | **Nest (mesic)** | **Matrix (mesic)** |
|---|---|---|---|---|---|---|
| **Carbon (%)** | 2,642 (±0,918) | 2,450 (±1,776) | 3,300 (±0,852)***** | 1,984 (±0,295)***** | 2,780 (±1,816) | 2,120 (±1,877) |
| **Calcium (cmol/mol)** | 11,087 (±11,680) | 9,008 (±6,013) | 14,639 (±15,330) | 7,545 (±6,355) | 11,570 (±6,114) | 6,447 (±5,250) |
| **Nitrogen (%)** | 0,198 (±0,082) | 0,179 (±0,118) | 0,241 (±0,093) | 0,154 (±0,041) | 0,210 (±0,126)***** | 0,147 (±0,113)***** |

Overall nest habitats had higher concentrations of C, Ca, and N than matrix habitats (Table 3.3), though none of these differences were signficant.

**Table 3.3.** The total mean (± standard deviation) concentrations of carbon, calcium and nitrogen in matrix and *Microhodotermes viator* nest habitats overall.

| | Nest | Matrix |
|---|---|---|
| **Carbon (%)** | 3,040 (±1,365) | 2,052 (±1,269) |
| **Calcium (cmol/mol)** | 13,104 (±11,121) | 6,991 (±5,525) |
| **Nitrogen (%)** | 0,226 (±0,106) | 0,150 (±0,080) |

However, at the site level, only nest habitats in Oudtshoorn and Worcester had higher C concentrations than their associated matrices, nest habitats in Koringberg and Worcester had higher Ca concentrations than their associated matrices, and nest habitats of Koringberg, Oudtshoorn and Worcester had higher N concentrations than their associated matrices. A detailed list of sites and concentrations is presented in Appendix F.

### 3.3.1. Frass quantification in Worcester

Each nest system had a huge amount of accumulated frass on its surface, this ranging between 234 – 827 kg/nest system (mound), with an average of 476 (±216.64) kg per nest. There was no relationship between nest system diameter and frass load (cor = -0.344; $p$ = 0.365). however using data of mean C, Ca and N concentrations in frass (from the leaching experiment) and mean frass load per nest system (476 kg) it was possible to calculate the mean enrichment of these elements per nest; C = 64.4 (±13.97) kg, Ca = 0.64 (±0.31) kg, and N = 3.65 (±1.74) kg for *M. viator* nests with a mean diameter of 20.17 (±3.16) m. The density of *M. viator* nests at Worcester where frass loads were quantified was 220 nests/km$^2$ (2.2 nests/ha$^{-1)}$ (Chapter 2). Using these values the estimated landscape enrichment of nutrients from frass at Worcester were C = 141.68 (±30.73) kg/ha$^{-1}$; Ca = 1.41 (±0.68) kg/ha$^1$; and N - 8.03 (±3.83) kg/ha$^{-1}$. Picker *et al*. (2007) determined the mean density of *M. viator* nests in the Western and Northern Cape Province to be 297 nests/km$^2$ (range 143 – 703 nests/km$^2$), which is similar to the mean of sites with high densities of *M. viator* nests determined in Chapter 2 (n = 39, Appendix A) of 304 nests/km$^2$ (range 143 – 720 nests/km$^2$). This equates to enrichment (kg/ha$^{-1}$) levels at different densities of *M. viator* as presented in Table 3.4.

**Table 3.4.** Estimated enrichment (kg/ha$^{-1}$) from *Micorohodotermes viator* frass at high and low-densities of nests (Picker et al. 2007) of carbon, calcium and nitrogen in areas of winter rainfall, South Africa.

| Nutrient | Low-density | High-density |
|---|---|---|
| **Carbon (kg/ha$^{-1}$)** | 92,09 (±19,98) | 463,68 (±100,58) |
| **Calcium (kg/ha$^{-1}$)** | 0,92 (±0,44) | 4,61 (±2,23) |
| **Nitrogen (kg/ha$^{-1}$)** | 5,22 (±2,49) | 26,28 (±12,53) |

### 3.3.2. Carbon, calcium and nitrogen profiles of nest and matrix soils

The mean concentration of C was significantly higher for nest soils in Oudtshoorn and Worcester than their associated matrix soils (Table 3.5.a). The mean concentration of Ca was significantly higher for nest soils in Koringberg and Worcester than their associated matrix soils (Table 3.5.a). The mean concentration of N was significantly higher in nest soils for Koringberg, Worcester and Oudtshoorn than their associated matrix soils (Table 3.5.a). The distribution of nutrient profiles is presented in an MDS ordination (Figure 3.2) which does not indicate any clear pattern or grouping, either for habitat (nest vs matrix) or location, indicating considerable variability in nutrient level across sites and habitat. Relative enrichment (expressed as a ratio) of *M. viator* nest soils at different sites was generally higher than that of the associated matrix, except in Malmesbury, where C and Ca were depleted in nest habitats and in Calitzdorp, where Ca and N were depleted in the nest habitats (Table 3.5.b).

**Table 3.5. a)** The mean concentration (±standard deviation) of carbon, calcium and nitrogen in *Microhodotermes viator* nest soils and their associated matrix soils at several sites across a rainfall (MAP) gradient. **b)** Relative enrichment of C, Ca and N from nest soils ($p < 0.05$ = *; $p < 0.01$ = **, Mann-Whitney U).

**a)**

| Site | Carbon (%) | | Calcium (cmol/mol) | | Nitrogen (%) | | MAP (mm) |
|---|---|---|---|---|---|---|---|
| | Matrix | Nest | Matrix | Nest | Matrix | Nest | |
| **Prince Albert** | 1,9140 (±1,8178) | 3,9780 (±2,9733) | 15,9840 (±17,5749) | 36,3540 (±26,0935) | 0,1866 (±0,1647) | 0,3235 (±0,1946) | 144,45 |
| **Vanrhynsdorp** | 2,2900 (±0,6330) | 2,5370 (±0,7962) | 4,1950 (±5,2344) | 5,2220 (±2,9319) | 0,1469 (±0,0830) | 0,1700 (±0,0642) | 162,88 |
| **Clanwilliam** | 2,1540 (±2,8271) | 4,0650 (±2,0504) | 12,4700 (±18,4850) | 25,3190 (±14,9992) | 0,1954 (±0,2342) | 0,3369 (±0,1473) | 182,2 |
| **Calitzdorp** | 2,044 (±1,225) | 2,2370 (±0,5228) | 3,9610 (±4,6188) | 2,1990 (±0,8858) | 0,1500 (±0,1024) | 0,1238 (±0,0289) | 244,73 |
| **Oudtshoorn** | 1,5180* (±0,5580) | 3,6810* (±1,8227) | 1,0640 (±0,9909) | 4,1010 (±3,3567) | 0,0916** (±0,03629) | 0,2498** (±0,1356) | 244,73 |
| **Worcester** | 0,4030** (±0,2563) | 0,9770** (±0,5540) | 1,8870* (±1,2167) | 13,6070* (±11,0453) | 0,0468* (±0,0327) | 0,0948* (±0,0498) | 285,79 |
| **Malmesbury** | 3,9750 (±1,7738) | 3,8010 (±2,3498) | 9,4990 (±10,4895) | 9,3500 (±7,2589) | 0,2876 (±0,1214) | 0,3186 (±0,1538) | 348,63 |
| **Koringberg** | 0,5160 (±0,2552) | 0,6860 (±0,3241) | 0,6250** (±0,3007) | 2,8630** (±3,4308) | 0,0269* (±0,0204) | 0,0614* (±0,0454) | 359,1 |
| **Tulbagh** | 4,2780 (±3,4281) | 4,6560 (±3,4066) | 6,9990 (±6,6403) | 12,4700 (±4,1969) | 0,2306 (±0,2028) | 0,3339 (±0,2437) | 777,65 |
| **Stellenbosch** | 1,4280 (±1,9300) | 3,7790 (±2,5000) | 13,2250 (±9,1410) | 19,5590 (±9,6983) | 0,1408 (±0,1415) | 0,2432 (±0,1629) | 1060,14 |

**b)**

| Site | Carbon | Calcium | Nitrogen |
|---|---|---|---|
| **Prince Albert** | 1:2.08 | 1:2.27 | 1:1.73 |
| **Vanrhynsdorp** | 1:1.11 | 1:1.25 | 1:1.16 |
| **Clanwilliam** | 1:1.89 | 1:2.03 | 1:1.72 |
| **Calitzdorp** | 1:1.09 | 1:0.56 | 1:0.83 |
| **Oudtshoorn** | 1:2.43 | 1:3.85 | 1:2.73 |
| **Worcester** | 1:2.42 | 1:7.21 | 1:2.03 |
| **Malmesbury** | 1:0.96 | 1:0.98 | 1:1.11 |
| **Koringberg** | 1:1.33 | 1:4.58 | 1:2.28 |
| **Tulbagh** | 1:1.09 | 1:1.78 | 1:1.45 |
| **Stellenbosch** | 1:2.65 | 1:1.48 | 1:1.73 |

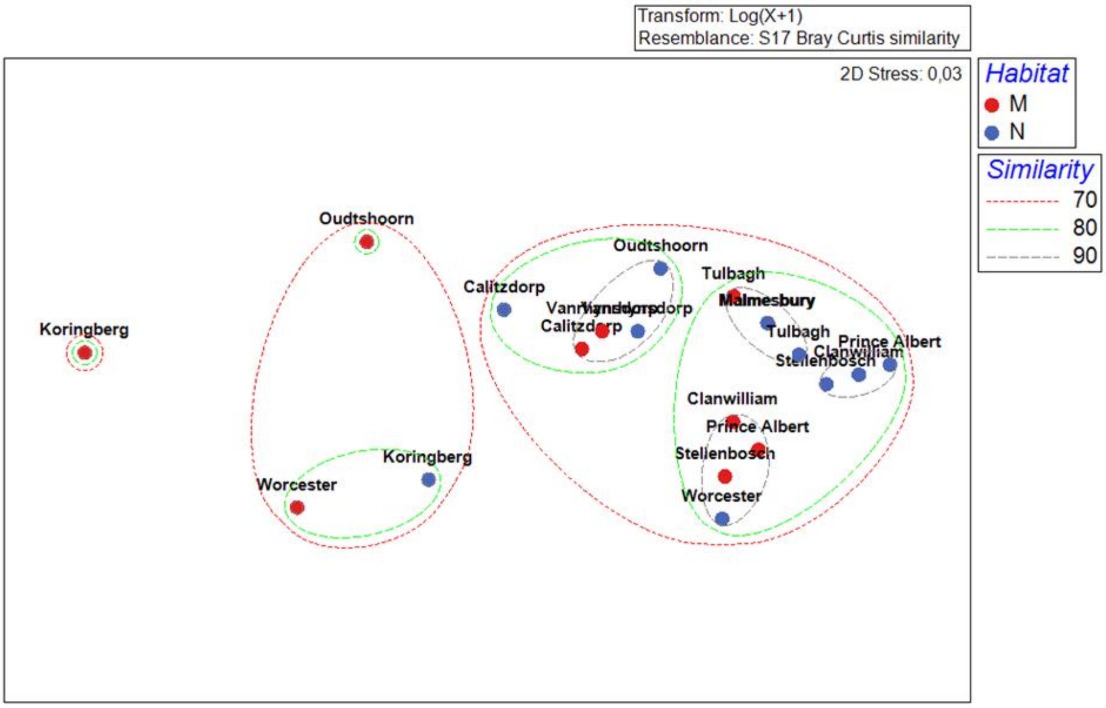

**Figure 3.3.** Bray-Curtis similarity Multi-dimensional Scaling (MDS) plot showing the distribution of nutrient profiles (carbon, calcium and nitrogen) of soils from *Microhodotermes viator* nests and their associated matrices from several sites.

The PERMANOVA indicated a significant difference between the mean soil nutrient profile of sites (F = 9.38, $p < 0.001$), and habitats (F = 15.10, $p < 0.001$) irrespective of site. The *post hoc* pairwise PERMANOVA test gives insight into how site-specific mean matrix- and nest soil nutrient profiles compare with others. Just over half (24/45) of the matrix soil nutrient profiles were significantly different from one another (Table 3.6.a). The matrix soil nutrient profiles of Koringberg and Worcester were significantly different to all others, except each other and Clanwilliam which was the least distinct among matrix soil nutrient profiles. Most (31/45) of the nest soil nutrient profiles were significantly different from one another (Table 3.6.b). That of Worcester was significantly different from all other sites, followed by Koringberg which was significantly different from all except Clanwilliam. The least distinct nest soil profile was that of Tulbagh which was only significantly different from half of the other sites. The mean nutrient profiles of only Koringberg, Oudtshoorn and Worcester showed a significant difference between habitats (Table 3.6.c).

**Table 3.6.** Pairwise posthoc analyses of the Permutational Multivariate Analysis of Variance showing the *p*-values (significant values in blue) for the difference in cumulative means of standardized nutrient concentrations between **a)** matrix soils of different sites, **b)** nest soils at different sites and **c)** different habitats (matrix vs nest) at each site.

**a)**

| | **CAM** | **CLM** | **KOM** | **MAM** | **OUM** | **PRM** | **STM** | **TUM** | **VAM** |
|---|---|---|---|---|---|---|---|---|---|
| **CLM** | 0,453 | | | | | | | | |
| **KOM** | 0,001 | 0,001 | | | | | | | |
| **MAM** | 0,011 | 0,254 | 0,001 | | | | | | |
| **OUM** | 0,091 | 0,146 | 0,001 | 0,001 | | | | | |
| **PRM** | 0,176 | 0,882 | 0,001 | 0,09 | 0,001 | | | | |
| **STM** | 0,159 | 0,651 | 0,001 | 0,019 | 0,012 | 0,73 | | | |
| **TUM** | 0,123 | 0,311 | 0,001 | 0,682 | 0,007 | 0,148 | 0,071 | | |
| **VAM** | 0,809 | 0,427 | 0,001 | 0,015 | 0,013 | 0,152 | 0,119 | 0,17 | |
| **WOM** | 0,001 | 0,003 | 0,074 | 0,001 | 0,001 | 0,001 | 0,003 | 0,001 | 0,001 |

**b)**

| | **CAH** | **CLH** | **KOH** | **MAH** | **OUH** | **PRH** | **STH** | **TUH** | **VAH** |
|---|---|---|---|---|---|---|---|---|---|
| **CLH** | 0,001 | | | | | | | | |
| **KOH** | 0,001 | 0,001 | | | | | | | |
| **MAH** | 0,004 | 0,09 | 0,001 | | | | | | |
| **OUH** | 0,018 | 0,011 | 0,001 | 0,354 | | | | | |
| **PRH** | 0,003 | 0,435 | 0,001 | 0,032 | 0,002 | | | | |
| **STH** | 0,002 | 0,327 | 0,001 | 0,201 | 0,059 | 0,186 | | | |
| **TUH** | 0,017 | 0,236 | 0,001 | 0,621 | 0,249 | 0,083 | 0,349 | | |
| **VAH** | 0,069 | 0,003 | 0,001 | 0,025 | 0,11 | 0,007 | 0,016 | 0,049 | |
| **WOH** | 0,001 | 0,001 | 0,01 | 0,001 | 0,001 | 0,004 | 0,006 | 0,008 | 0,001 |

**c)**

| | | | |
|---|---|---|---|
| **Calitzdorp (CA)** | 0,6430 | **Prince Albert (PR)** | 0,0570 |
| **Clanwilliam (CL)** | 0,1020 | **Stellenbosch (ST)** | 0,0660 |
| **Koringberg (KO)** | 0,0340 | **Tulbagh (TU)** | 0,4180 |
| **Malmesbury (MA)** | 0,9090 | **Vanrhynsdorp (VA)** | 0,5780 |
| **Oudtshoorn (OU)** | 0,0004 | **Worcester (WO)** | 0,0010 |

The cumulative enrichment profiles of bush-clumps, mounds of other termite species, and heuweltjies were compiled in Table 3.7. The nitrogen concentrations between all samples were similar, and the carbon concentration of heuweltjies higher than that of bush-clumps of mounds of other termite species. Interestingly the concentrations of P, K, Ca and Mg measured in mounds of other termite species and heuweltjies were similarly higher than that measured for bush-clumps.

**Table 3.7.** Comparing ratios of nutrients on bush-clumps, termite mounds, and heuweltjies compared to their associated matrices using values from literature and this study using the median (first and third quartile, n).

| Nutrient | Bush-clumps[2,3,4,8] | Termite mounds[5,6,7,11] | Heuweltjies[1,9,10,12] |
|---|---|---|---|
| **Nitrogen** | 1.40 (1.11, 1.76, 18) | 1.28 (1.18, 1.38, 5) | 1.68 (1.52, 1.94, 3) |
| **Phosphorus** | 1.52 (1.30, 2.48, 17) | 2.26 (1.36, 3.67, 7) | 4.51 (2.96, 9.26, 3) |
| **Potassium** | 1.48 (1.13, 1.59, 17) | 2.93 (2.16, 3.28, 3) | 2.84 (2.54, 3.14, 2) |
| **Carbon** | 1.44 (1.22, 1.78, 7) | 1.29 (1.14, 1.33, 5) | 2.05 (1.88, 3.61, 3) |
| **Calcium** | 0.97 (0.89, 1.02, 16) | 3.31 (1.01, 8.73, 7) | 2.60 (2.55, 7.89, 3) |
| **Magnesium** | 0.92 (0.90, 1.06, 17) | 4.00 (2.38, 4.95, 7) | 5.47 (5.29, 5.65, 2) |

(Midgley and Musil, 1990[1]; Schlesinger *et al*., 1996[2]; Jarvel and O'Connor, 1999[3]; Escudero *et al*., 2014[4]; Holdo and McDowell, 2004[5]; Ackerman *et al*., 2007[6]; Sarcinelli *et al*., 2009[7]; Abanda *et al*., 2011[8]; Kunz *et al*., 2012[9]; Francis *et al*., 2013[10]; Seymour *et al*., 2014[11]; This study[12])

### 3.3.3. Nutrient leaching from frass packs

The data exhibited multi-collinearity and were thus not suitable for MANOVA analysis, and were instead subjected to standard tests (paired Student T-test or paired Mann-Whitney U) for calculation of the difference in means. Mean concentrations of C, N (t-test), and Ca (Mann Whitney U) were significantly higher ($p < 0.05$) in frass than soil upon both before and after the experiment (Figure 3.3). Frass consistently had higher concentrations of C (start = 13.53 %; end = 14.79 %), Ca (start = 1.20 %; end = 1.18 %), and N (start = 0.77 %; end = 0.67 %) at both the start and end of the experiment compared to soil (C, start = 2.98 %; end = 2.45 %; Ca, start = 0.29 %; end = 0.12 %; N, start = 0.22 %; end = 0.14 %). The difference in the mean concentration of Ca in the soil before and after the experiment indicate a significant ($p < 0.05$, Student T-test) loss of 0.0018 g Ca per gram (0.18 %) of soil during the experiment (Figure 3.5.b, S3). The difference in the mean concentration of N in frass before and after the experiment indicate a significant ($p < 0.05$, Student T-test) loss of 0.0010 g N per gram (0.10 %) frass during the experiment.

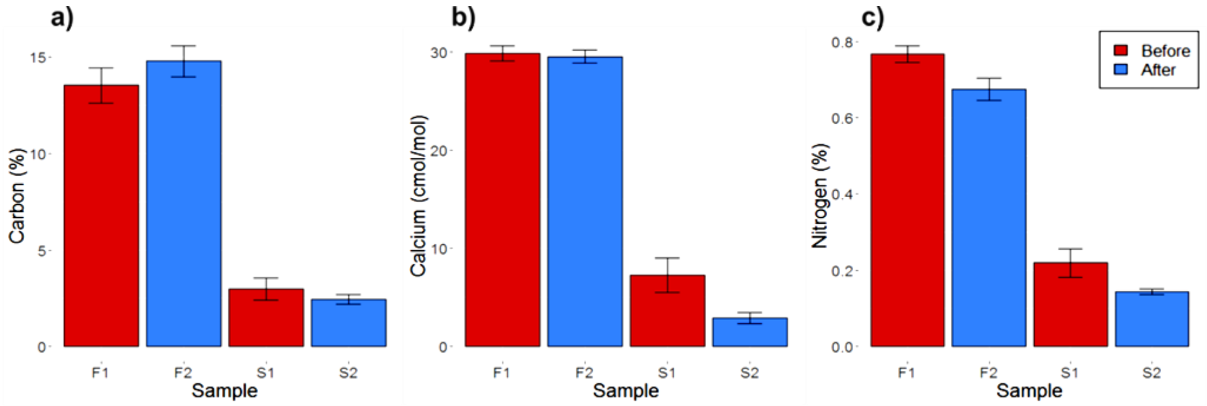

**Figure 3.4.** The mean and standard deviation of a) Carbon, b) Calcium and c) Nitrogen concentration in frass before (F1) and after (F2) the experiment, and in the soil before (S1) and after (S2) the experiment.

An NMDS ordination using all the available nutrient data for Worcester from this study (frass n = 18, matrix n = 28, and nest n = 10) (Figure 3.4) showed some clustering for each sample type. Bray-Curtis similarity percentage (SIMPER) and Analysis of Similarity (ANOSIM) were calculated. These results determined that nutrient profiles of frass and nest soils were most similar (60 %), followed by nest and matrix soils (58 %). Nutrient profiles of frass and matrix soils were the least similar (33 %).

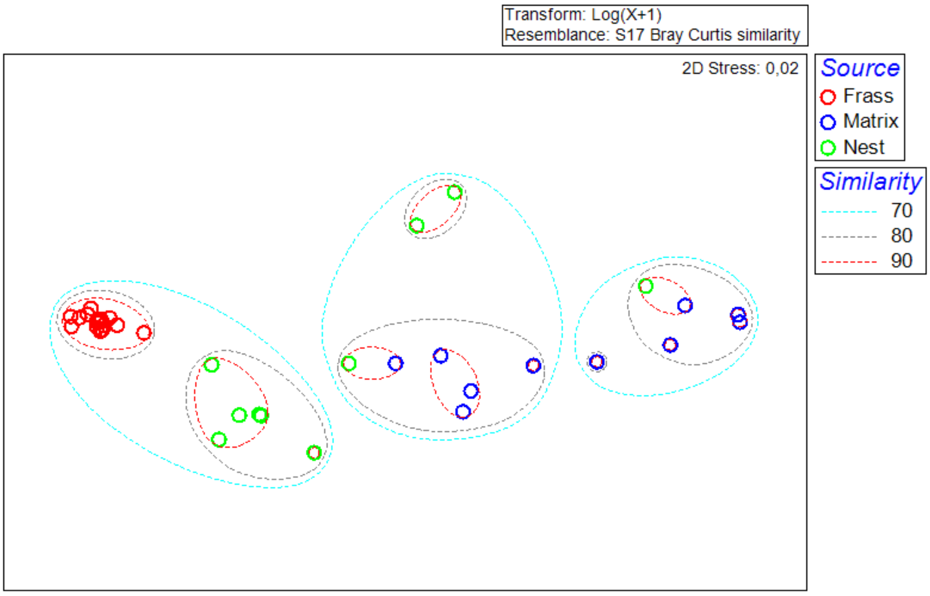

**Figure 3.5.** Bray-Curtis similarity visualized in a Non-Metric Multi-Dimensional Scaling (NMDS) plot clustering the soil nutrient profiles (carbon, calcium and nitrogen) of frass (n = 18), matrix (n = 38) and nest soils (n = 10) at Worcester.

## 3.4. Discussion

### 3.4.1. Frass production by *M. viator*

This study was a unique attempt at quantifying the amount of frass associated with a very large termite nest system. The rate of frass production could not be measured as, during the study period (18 months), very little (scattered) frass was deposited on mounds that had been cleared. Low rainfall and prevalent drought conditions during this period likely resulted in decreased termite activity and subsequently reduced foraging by *M. viator* (McAuliffe *et al.*, 2019), limiting frass production during this period. Food collection and processing (and thus frass production) are likely more intense in winter when temperatures decline, soils become moist and plant productivity increases. However, it would appear that the substantial frass deposits measured on each mound were likely the result of many years' accumulation given the minute quantities of new frass generated after removal of the substantive piles of accumulated frass. However, the hive of *M. viator* can extend to a metre in diameter (Coaton, 1958) so the accumulation of the vast quantities of frass observed are consistent with the large colony size.

The contribution of C (141.68 kg.ha$^{-1}$), Ca (1.41 kg.ha$^{-1}$) and N (8.03 kg.ha$^{-1}$) from superficially deposited *M. viator* frass to soil fertility was considerably higher than C (1.72 kg.ha$^{-1}$), Ca (0.15 kg.ha$^{-1}$), and N(0.15 kg.ha$^{-1}$) reported for *M. bellicosus* (Abe *et al.*, 2009), where nest soils and not frass was examined. However, only the uppermost soil horizons of *M. bellicosus* nests, from which nutrients are dispersed to the surrounding landscape, contribute to enrichment. This equates to only 0.5 % of the enrichment from *M. bellicosus* described above. Nutting *et al*. (1987) determined the mean amount of soil transported to the surface by *Heterotermes aureus* to be 70.3 kg.ha.year$^{-1}$ and by *G. perplexus* to be 574.9 kg.ha.year$^{-1}$ and, where their territories overlap, the two species together transport 99.0 kg.ha.year$^{-1}$. The annual enrichment values of both *H. aureus* and *G. perplexus* are considerably less than that of *M. viator* frass loads in Worcester and support the statement that the mean frass load (476 kg) on *M. viator* nests in Worcester accumulated over a long period of time. The subsequent enrichment from frass has profound effects on local vegetation, which is discussed in Chapter 5.

### 3.4.2. Nutrient enrichment by *M. viator* across a rainfall gradient

Higher mean nutrient concentrations (C, Ca, N) were observed in the nest than in matrix soils at all sites except Calitzdorp, where Ca and N concentrations were slightly higher in the matrix than nest soils, and at Malmesbury, where Ca and C concentrations were higher in the matrix than nest soils (Table 3.5.a). Since *M. viator* mounds are known as sites that experience soil perturbation, the sampled nest soils are likely a mixture of topsoil and subterranean horizons and mound structures brought about by the burrowing activity of mammals (Louw *et al.*, 2017) increasing noise in the composition of the sampled mound soil.

Lower levels of enrichment were expected at low rainfall (MAP < 245 mm) sites because low rainfall would result in fewer nutrients being mobilized for plant uptake. This was true for mean N (1.64) and Ca (1.99) enrichment at low-rainfall sites, compared to that of high-rainfall (MAP > 286 mm) sites (N = 1.72; Ca = 3.21). However, the mean enrichment of C was lower in high-rainfall (1.69) compare to low-rainfall sites (1.72) despite the greatest C enrichment (2.65) being found in a high-rainfall site, Stellenbosch.

This might be explained by the considerable range (284 – 1060 mm) of rainfall at high rainfall sites compared to low (145 – 245 mm) rainfall sites. However, pre-existing differences in matrix soils between sites would affect levels of enrichment, with more fertile sites (on decomposed granite and shale) providing less contrast than that observed when mounds are on nutrient-poor soils such as sandstone. Just as McAuliffe *et al*. (2019) hypothesized that there is a climatic “*Goldilocks zone*” for the formation of heuweltjies, which is not too dry, nor too wet, it is likely such a zone exists for enrichment and would explain the high enrichment at medium rainfall sites. Enrichment, in this case, is tied to *M. viator* activity, which is less at low rainfall, where there is less plant matter to forage and mounds might contain smaller colonies. At high rainfall sites where vegetation is more abundant, it is possible that nutrient leaching from frass becomes more readily available to plants, promoting denser and abundant plant growth in the matrix, which in turn provide enrichment with the breakdown and decay of dead plant material and dung of attracted herbivores. The increased nutrient concentrations from increased plant cover smoothes the gap in matrix and nest nutrient concentrations to some extent, reducing the amount of enrichment provided by *M. viator*.

At intermediate rainfall sites, there is likely optimal *M. viator* activity, and a “*golden middle*” in plant cover, where the contrast in matrix and nest soil enrichment is most visible. These different enrichment-rainfall patterns have different effects on plant diversity and community composition (Mucina and Rutherford, 2006; Hoffmann *et al.*, 2012), and distinct nutrient profiles between nest and matrix habitats will have significant effects on landscape heterogeneity (Joseph *et al.*, 2011; Muvengwi and Witkowski, 2020). As discussed in Chapter 1 and partly in this section, rainfall will influence the availability of nutrients. For higher rainfall areas the nutrients become more readily available for plant uptake, possibly leading to increased growth, density and diversity of plants, which in turn leads to increased foraging by *M. viator,* larger colonies and increased levels of enrichment by *M. viator*. These mechanisms and their impact on plant community composition are explored in more detail in Chapters 4 and 5.

### 3.4.3. Carbon, calcium and nitrogen enrichment by *M. viator* in matrix soils

The frass packs experienced a small (0.45 g) but significant loss in N, and soil a loss of 0.002 g mean Ca. The lack of substantial leaching can be ascribed to conditions at the site where packs were distributed in the matrix for 15 months. The site experienced below-average (309 mm) rainfall during these 15 months, compared to a mean of 354 mm for 10 years before this experiment (SAWS, 2018). In addition, the site only had four daily rainfall measures above 15 mm; 15.6 mm on 21 May 2018, 40.2 mm on 14 June 2018, 36.0 mm on 1 July 2018, and 18.8 mm on 25 August 2018, with maximum daily temperatures of 19.6, 21.5, 20.1, and 17.5° C respectively (SAWS, 2018). On low rainfall days, it is possible water evaporated before any significant leaching could occur. It is also possible that the total rainfall on higher days was the sum of several small, short rainfall events on the day and might similarly be evaporated before any significant leaching could occur. Lastly, the nature of the leaching from frass might simply require a lengthier period due to the nature of the frass itself. Old frass dumps of heuweltjies become grey and then whitish, suggestive of leaching of some constituents, leaving the very high Ca levels behind. Nutrients bound in fresh *M. viator* frass might become more soluble and readily transported/leached over a far lengthier time frame, as illustrated in nests of *G. perplexus,* where nutrients are released within weeks/months from nest soils after the first heavy rains, compared with that of *H. aureus,* where leaching can take years (Nutting *et al.*, 1987). In addition, the lack of physical soil modification by *M. viator* means that matrix soil surfaces were not conducive to water infiltration and leaching and the rate of leaching in the matrix would be significantly lower than on nests (matrix water infiltration is compared with that of nest soils in Worcester in Chapter 4) (Carnol and Ineson, 1999). This suggests that, even if comparable nutrient enrichment from vegetation clumps could be measured, the physical modification of soil as produced by termites would still be lacking and enriched nutrients would not be as readily available to plants.

The only parallel to this experiment examined the rate and concentration of nutrients leached through entire nests (Rückamp *et al.*, 2009). Using free-draining lysimeters installed below abandoned young nests of *Cornitermes silvestri*, older nests secondarily inhabited by *Nasutitermes kemneri*, and reference matrix soils, they found that the volume of drained water was significantly more in reference soils. This is attributed to the primary termite inhabitant *C. silvestri,* which builds nests with hard crusts and inhibits water infiltration. Drainage water collected in lysimeters below nests however revealed significantly more nitrate in nests secondarily inhabited by *N. kemneri* (2.13 ±1.35 mg N litre$^{-1}$) than primary inhabited nests (0.61 ±0.28 mg N litre$^{-1}$) or reference soils (0.60 ±0.27 mg N litre$^{-1}$). The higher nitrate concentrations in secondarily inhabited nests, compared to that of primary inhabited nests and reference soils, can be attributed to the behaviour of *N. kemneri* of enriching nests with nitrate 2 - 42 times that of reference soils (Ndiaye *et al.*, 2004; Rückamp *et al.*, 2009). The authors found no significant difference in pH, mean concentrations of dissolved organic carbon (DOC), phosphate, or ammonium between water drained from reference soils and primary- and secondarily inhabited nests. They attribute the lack of significant difference in DOC concentration between treatments to longer drainage paths in nests (from the top of the nest to the lysimeter) compared to reference soils, which increases DOC adsorption and mineralization (Rückamp *et al.*, 2009).

The nutrient profile of nest soils is derived from that of matrix soils exposed to physical and chemical modification by *M. viator* (Moore and Picker, 1991; McAuliffe *et al.*, 2019). One mechanism for chemical change is the incorporation of frass into the matrix soil, and thus the nest soil nutrient profile would show significant similarity to both the nutrient profiles of matrix soil and frass. Given the slightly higher similarity of nest soils with frass of *M. viator* than with matrix soils (Figure 3.4) and the high dissimilarity between the latter two, it is reasonable to equate the nutrient profile of *M. viator* nest soils with that of heuweltjies (Table 3.7). The nutrient profile of heuweltjies (Midgley and Musil, 1990; Kunz *et al.*, 2012; Francis *et al.*, 2013), including values obtained in this study, show similar enrichment of N to bush-clumps (Schlesinger *et al.*, 1996; Jarvel and O'Connor, 1999; Escudero *et al.*, 2004; Abanda *et al.*, 2011) and mounds of other termite species (Holdo and McDowell, 2004; Ackerman *et al.*, 2007; Sarcinelli *et al.*, 2009; Seymour *et al.*, 2014), but greater C enrichment. However, the enrichment levels of P, K, Ca and Mg are similarly higher on heuweltjies and mounds of other species compared to bush-clumps. Thus the literature to date is unable to present similar levels of enrichment between bush-clumps and heuweltjies but is able to provide similar enrichment levels between heuweltjies and mounds of other termite species further supporting the termite origin theory for heuweltjies.

### 3.5. Conclusion

The argument that "*heuweltjies*" (considered here and by McAuliffe *et al*. 2019 as nest systems of *M. viator*) are the accumulation of litter decomposition from clumping of woody shrubs (Cramer *et al.*, 2012) is not supported by the levels of enrichment from leaf litter that could generate the levels of enrichment seen in *M. viator* nest systems, particularly in the case of Ca. Following the hypothesis of Cramer *et al*. (2012) proposing heuweltjie formation as a result of bush-clumps resistant from different erosion taking place in the matrix McAuliffe *et al*. (2014) instead proposed the hypothesis of successive aeolian sediment accretion on vegetation clumps formed in response to enrichment as a result of *M. viator* activity. The association of *M. viator* was based on the termites' ability to accelerate the formation of a calcic horizon, characteristic of heuweltjies, by foraging for and transporting calcium-rich plant materials and accumulating them. Cramer & Midgley (2015) supported the hypothesis of aeolian sediment accretion to form heuweltjies, but argued that the over-dispersion of heuweltjies was not consistent with *M. viator* spatial patterning, but instead the result of vegetation patterning. In addition, this study provides evidence that nutrient profiles of *M. viator* nests are similar to those of several other termite species (Figure 3.5) and shows a higher degree of similarity than matrix soils with frass.

The monitoring of frass loads on *M. viator* nests to determine the rate of production, and also the rate of nutrients leached from frass will require long term monitoring. Future frass-nutrient leaching experiments should include replication in nest and control reference soils in addition to matrix soils, to replicate naturally-occurring heterogeneity in physical soil characteristics across an extended period. The involvement of *M. viator* in nutrient enrichment will get further confirmation by comparing nutrient profiles of *M. viator* nests beyond the distribution of heuweltjies, with that of heuweltjies and other manifestations of *M. viator* nests within its distribution range. Nutrient enrichment, as demonstrated in this study, can promote plant growth and productivity (Seymour *et al.*, 2014; McAuliffe *et al.*, 2019). Improved plant productivity attracts fauna, either by providing a nutrient-rich, dense food source or shelter (McAuliffe *et al.*, 2019). Selective grazing by sheep on heuweltjies has been demonstrated (Armstrong and Siegfried, 1990). In addition, a higher association has been demonstrated with mammals such as steenbok (*Raphicerus campestris*) that use them as middens (Milton and Dean, 1990), aardvark (*Orycteropus afer*) that forage for termites (Milton and Dean, 1990; Louw *et al.*, 2017), and greater associations with spiders (Henschel and Lubin, 2018) and ants (Arena *et al.*, 2020) than in the corresponding matrix.

# CHAPTER 4 – WHY DO NEST SYSTEMS OF *MICROHODOTERMES VIATOR* SUPPORT DISTINCTIVE PLANT COMMUNITIES?

## 4.1. Introduction

At a global scale, plant community structure is determined by evolutionary and biogeographic constraints, driven by mechanisms of dispersal and vicariance (Carlquist, 1983; Wiens and Donoghue, 2004; Trénel *et al.*, 2007). Climate and soil drive terrestrial plant community structure at the global biome scale (Lomolino *et al.*, 2010), while climate, soils, topography and disturbance drive species distribution and community composition at a regional biome scale (Mucina and Rutherford, 2006; Hoffmann *et al.*, 2012). At the local (landscape) scale other factors drive heterogeneity in plant communities, one of these being nest-building activities of social insects (Dangerfield *et al.*, 1998; Moe *et al.*, 2009; Joseph *et al.*, 2013; Seymour *et al.*, 2014; Muvengwi, 2017).

Termite nest systems often support denser vegetation, distinct in composition and structure from that of the surrounding matrix. In the grasslands of the Free State of South Africa, the highest density of vegetation has been found on old-active nests of the harvester termite *Trinervitermes trinervoides*. The density of grasses gradually decreased from young-active nests, through partially-abandoned and abandoned nests, to eroded nests – a pattern reflective of the combined effects of termite-associated nutrient enrichment, grass growth responses and preferential grazing by mammals (Smith and Yeaton, 1998). In addition, the species composition of plants associated with active, inactive and eroded nests of *T. trinervoides* was different from that of the matrix. However, young-active nests and inactive nests had similar vegetation composition. In West African savannas vegetation on nests of *Macrotermes* sp. also differed from that of the surrounding matrix. Here the difference in nest and matrix vegetation was correlated with termite-induced clay enrichment and increased cation concentrations in the vicinity of the nest, which became increasingly pronounced at higher (MAP) rainfall (Erpenbach *et al.*, 2013).

Differences in soil conditions (pH, electric conductivity, clay content and nutrients) between termite (Macrotermitinae) nests and the associated matrix have been identified as prominent drivers that result in distinct plant community compositions between these two habitats in the Miombo woodlands of Zimbabwe (Joseph *et al.*, 2013). A similar pattern has emerged in African savannas for nutrient enrichment of nests of *Ancistotermes* spp., *Cubitermes* spp. *Macrotermes* spp. *Odontotermes* spp. and *Trinervitermes* spp. and vegetation heterogeneity (Sileshi *et al.*, 2010). Nest-plant communities may be additionally influenced by other local disturbance regimes that affect the nest or matrix in different ways e.g. preferential herbivory on nests, or fire in the matrix (Holdo and McDowell, 2004; Sileshi *et al.*, 2010).

The soil properties of *Microhodotermes viator* nests, including nutrient concentration (Chapter 3) and water holding capacity, differ from those of the surrounding matrix (Midgley and Musil, 1990; Milton and Dean, 1990; Lovegrove, 1991; Booi, 2011; Kunz *et al.*, 2012) resulting in the development of distinct plant communities on nests, compared to the surrounding matrix (Knight *et al.*, 1989; Rahlao *et al.*, 2008; Schmiedel *et al.*, 2016). In high-rainfall areas with greater water availability and greater plant biomass, plant community composition of *M. viator* nests is explained primarily by the increased nutrient concentrations (Campbell and Werger, 1988; Picker *et al.*, 2007). In low-rainfall areas, however, water is the limiting factor necessary for efficient nutrient uptake (Caldwell *et al.*, 1998; Carnol and Ineson, 1999). Even with increased nutrient concentrations on nests, the enrichment is not likely to be expressed in a water-deficient system, and the nest vegetation is dominated by succulents that are better able to tolerate water deficits (Booi, 2011; Seymour *et al.*, 2019). In these systems, soil salinity is likely the greatest contributor to vegetation type and dynamics (Francis *et al.*, 2007; Booi, 2011).

However, the mechanism by which the different nest and matrix soil properties drive the development of distinct plant communities, e.g. the factors responsible for the dominance of *Pteronia incana* on *M. viator* nests and the dominance of the closely-related *P. paniculata* in the surrounding matrix at the study site at Worcester (Rahlao *et al.*, 2008), is not as well understood. Different life-history characteristics related to seed germination and/or growth in response to different soil properties may drive this distinction and are examined in this chapter.

### 4.1.1. Germination as a function of soil nutrient concentration and soil-water properties in arid ecosystems

Soil conditions (water, conductivity, temperature, light and chemistry) initiate germination by triggering the production of growth hormones (De Villiers, 2000; Nabors, 2004) during times when conditions for seedling growth would be optimal (Badger and Ungar, 1989; Jurado and Westoby, 1992; Probert, 1992; De Villiers, 2000). These environmental cues required to initiate germination are species-specific (Datta, 1965; Hobson, 1990; De Villiers, 2000) and subject to developmental and genetic adaptation (Freeman *et al*., 1977; Gutterman, 1993; 2000).

The pericarp and/or testa of seeds, especially of arid plant species, often contain water-soluble germination inhibitors (Gutterman, 1993; Van Rooyen and De Villiers, 2004). When sufficient rainfall occurs and the inhibiting substance is dissolved, imbibition can occur to facilitate germination (Lambers *et al.*, 2008). The osmotic potential, which can either facilitate or prevent imbibition, is subject to soil conductivity, which also can have toxic effects on seed viability when levels are beyond the range of tolerance (Hobson, 1990; Kaymakanova, 2009).

Experiments on the germination of eight species of African leafy vegetables determined the optimal temperature for germination to be between 25 – 31 °C (Motsa *et al.*, 2015), while several species in the Succulent Karoo were found to germinate optimally between 15 – 20 °C which coincides with ambient temperatures of the winter rainfall region in which they occur (Henrici, 1935; Van Rooyen and De Villiers, 2004).

The effects of light have been investigated for several species and vegetation types (Gutterman, 2000; De Villiers *et al.*, 2002; Schütz *et al.*, 2002; Van Rooyen, 2002; Kulkarni *et al.*, 2007; Motsa *et al.*, 2015) and found to be highly variable. However, it is often found that species with small seeds having limited resources cannot successfully emerge when buried too deep (Schütz *et al.*, 2002; Van Rooyen, 2002; Van Rooyen and De Villiers, 2004). The mechanism by which small seeds can determine their burial depth is light detection. Upon detection of sufficient light, germination is initiated, while the absence of light will prolong dormancy for a species-defined period (Bell, 1993; Plummer and Bell, 1995; Bell, 1999; Van Rooyen and De Villiers, 2004).

When a plant dies, uptake of N from the soil by the plant ceases and the dead plant decomposes, while mineralization and nitrification continue and eventually increase the soil N concentration (Van Rooyen and De Villiers, 2004; Lambers *et al.*, 2008). This higher N concentration is considered a mechanism by which seeds can detect a spatial gap and an opportunity to grow (Pons, 1989). Similar triggers of germination have been detected for seeds stimulated by plant-derived smoke (Pierce *et al.*, 1995; Thomas and Van Staden, 1995; Strydom *et al.*, 1996). The concentration of compounds such as ammonia and octanoic acid, which increase due to smoke from plant-derived fires, are considered cues to stimulate seed germination when vegetation is removed by fire and competition for space is absent or significantly reduced (Lambers *et al.*, 2008). It has been established that seeds generally germinate optimally in soils with a pH of 7, and tolerate a range ±2 beyond which germination sharply declines (Chartzoulakis and Loupassaki, 1997; Roem *et al.*, 2002; Pérez-Fernández *et al.*, 2006; Laghmouchi *et al.*, 2017). However, the use of different chemical solutions with similar pH on the same germination media have resulted in different outcomes of germination success and rates (Gupta and Basu, 1988; Foley and Chao, 2008) and it has been suggested that the observed effects of soil pH on germination success and rate are influenced by additional chemical interactions (Ma *et al.*, 2015)

Van Rooyen and De Villiers (2004) recognized three groups of species based on their germination responses to light 1) stimulated, 2) inhibited, and 3) unaffected by light, and also noted that these responses could further vary, based on different temperatures. The combination of these varying effects of the interaction between light and temperature on seed germination has been demonstrated several times (De Villiers *et al.*, 2002; Kambizi *et al.*, 2006; Qu *et al.*, 2008; Motsa *et al.*, 2015). The positive relationship between salinity of soil and osmotic pressure in seeds has been well documented and represents the interaction between water and salinity in the germination process (Bradford, 1995; Kang and Saltveit, 2002; Ramin, 2006; Laghmouchi *et al.*, 2017). This interaction in turn affects chemical solution in soils and pH (Gupta *et al.*, 1989; Al-Busaidi and Cookson, 2003). An additional interaction between high salinity and respiration in the absence of light was noted in the germination and growth of bean plants - the stage (germination or early growth) at which this interaction occurs, however, is unclear (Kaymakanova, 2009).

Germination success as a function of nutrient concentrations is poorly understood, especially in arid ecosystems. However, it is known that chemical signals, such as low-nitrate conditions in the soil, can maintain dormancy until favourable conditions occur (Van Rooyen and De Villiers, 2004; Lambers *et al.*, 2008). In a greenhouse experiment, seeds of four plant species native to each habitat (viz. *M. viator* nest and matrix) from two sites (Prince Albert and Worcester) were established in reciprocal treatments of soil from the two habitats (Riginos *et al.*, 2005). All species germinated successfully in both treatments, except *Ruschia caroli,* which had poor germination in both treatments.

Although comparative examples in arid ecosystems are lacking, it has been demonstrated in mesic ecosystems that nutrients could differentially influence the germination of different plant species and therefore alter community composition. The addition of a Ca solution to experimental heathland germination plots in the Netherlands significantly improved the germination success of *Succisa pratensis*, *Parnassia palustris* and *Euphrasia stricta*, and the addition of an Al solution was detrimental to the germination success of all species investigated. These effects were linked to the respective increase in pH as a result of Ca enrichment and decrease in pH as a result of Al enrichment. (Roem *et al.*, 2002). In freshwater wetlands in the Everglades, replacement of sawgrass (*Cladium jamaicense*) in patches with two cattail species (*Typha domingensis* and *T. latifolia*) was observed in response to changes in water phosphate concentrations (Stewart *et al.*, 1997). The two

*Typha* spp. had similar germination success under phosphate enrichment, but *T. domingensis*, plants showed enhanced growth, bearing more flowering shoots and thus dominated *T. latifolia in situ*. However, *T. latifolia* had a competitive advantage over *T. domingensis* at lower nutrient concentrations, being able to germinate faster.

Furthermore, seeds of tomato and lettuce soaked in treatments of distilled water (control) and a solution of vermicompost (enrichment of N, P, K, Ca and Mg) showed significantly higher germination success for seeds soaked in the vermicompost solution. This suggests that, beyond a requirement of soaking to soften hard seed coats and to neutralize chemical germination inhibitors in the seed, other chemical factors were involved in improved germination success and growth (Türkmen *et al.*, 2004; Arancon *et al.*, 2012). Despite no difference in germination excess noted in the arid example from Prince Albert and Worcester (Riginos *et al.*, 2005), it was found that the emergent seedlings grew faster in soils from *M. viator* nests compared to those in matrix soils, likely a result of the enriched nest soils.

### 4.1.2. Transplanted seedling growth responses to soil nutrient concentration and soil-water properties

Following the dissolution of water-soluble germination inhibitors surrounding some seeds (Gutterman, 1993; Van Rooyen and De Villiers, 2004) water is absorbed and plays an essential role in early seedling growth as a component of molecules (proteins, nucleic acids, carbohydrates) that are of biological importance (Hopkins and Hüner, 2004). The impact of water on seedling survival was demonstrated in a three-year (1989 - 1991) study of seedlings in the Succulent Karoo (Prince Albert), during which survivorship was greatest (25 %) in 1991 which experienced additional winter and spring rains compared to the former two years (< 5 % survival) (Milton, 1995). Water is also responsible for reduced thermal stress and improved mobilization of nutrients (Hopkins and Hüner, 2004; Lambers *et al.*, 2008), which are beneficial to early seedling establishment and persistence (Seymour *et al.*, 2019).

In the Succulent Karoo, long-term (20 y) supplemental N, K, and N-K experiments found that N supplementation generally increased plant cover (a proxy for growth) at the cost of cover stability, while K supplementation improved cover stability of short-lived plant species and could moderate changes induced by N supplementation (Seymour *et al.*, 2019). The correlation of community composition (canonical coefficient) with N-supplementation - both alone and with K-supplementation, compared to the correlation of community composition of K-only supplementation (control), indicated that additional N was associated with changes in cover (proxy for growth), the stability of cover, and plant community composition (Seymour *et al.*, 2019). Short-lived plant species characteristic of *M. viator* nest vegetation cover in the Succulent Karoo (*Mesembraynthemum noctiflorum* and *M. vaginatum*) were among the species for which cover increased with N-supplementation so that fertilized plots became similar in composition to *M. viator* nests. However, some species not associated with nest habitats, (*Ruschia spinosa* and *Drosanthemum praecultum*) also increased in nitrogen addition trials. There was also a trade-off in response to increased N concentrations, whereby seedlings of *Osteospermum sinutaum* experienced faster above-ground growth, but greater mortality (Seymour *et al.*, 2019). This supports the idea that the different plant communities of *M. viator* nests and the matrix in Prince Albert are partially driven by differences in soil N and K concentrations.

Van Der Waal *et al*. (2009) determined that competitive effects of herbaceous plants (*Brachiaria deflexa*, *Melinis repens*, and *Urochloa mosambicensis*) on woody seedlings (*Colophospermum mopane*) in South African savannas remained constant with increasing water availability, but they hypothesized that competition would increase during drought conditions. This study also determined that the competitive effect of herbaceous plants on woody seedlings increased when enriched with commercial NPK fertilizer. Competitive interactions between plants in arid systems are driven by light, soil or water, or combinations of these resources (Nobel, 1989; Reichenberger and Pyke, 1990; Holmgren *et al.*, 1997). On the contrary, plants may have a facilitative effect whereby seedlings are protected from herbivory (Ibáñez and Schupp, 2001; Rebello *et al.*, 2005), or provided greater soil nutrients (Nobel, 1989), improved soil water conditions (Barnes and Archer, 1999), and reduced thermal stress and evapotranspiration (Franco and Nobel, 1988; Greenlee and Callaway, 1996).

Reciprocal transplant experiments conducted in Prince Albert (low-rainfall) and Worcester (high-rainfall) found species-specific differences in survivorship between seedlings transplanted on *M. viator* nests and seedlings transplanted in the matrix (Riginos *et al.*, 2005). Nests of *M. viator* are well known to have different soil conditions (higher nutrient concentrations and water content), which are considered primary drivers for differences in the respective plant communities, compared to the associated matrix (Midgley and Musil, 1990; Herpel, 2008; Kunz *et al.*, 2012; Bekker *et al.*, 2016). Greater survival was found for all species on nests compared to the matrix, however, at both sites, species-specific differences were detected for the interactions of, and survivorship between seedlings grown close to mature shrubs, and seedlings grown in cleared plots. These findings suggested that the effects of rainfall and nutrients influence interactions (competitive and/or facilitative) between mature plants and seedlings, and require more complex models (Riginos *et al.*, 2005) to explain the relationship between plant interactions and soil properties. Changes in the chemical composition and water-holding capacity of soils not only alter germination and growth rates but in-so-doing may lead to changes in competitive interactions that ultimately shape vegetation composition and structure.

### 4.1.3. Objectives

Distinct plant communities are a feature of *M. viator* nests and are purportedly associated with soil changes (nutrient enrichment and increased soil porosity) produced by termite activity (Knight *et al.*, 1989; Midgley and Musil, 1990; Rahlao *et al.*, 2008). However, proximal factors underlying this distinction have not been investigated. Termite (and ant) nests have been reported as sites associated with higher seedling densities, compared to the rest of the Karoo landscape (Dean and Yeaton, 1992; Milton, 1995). Although no studies have linked species-specific differences in germination success of Karoo plant species with soil differences, this has been demonstrated elsewhere (Roem *et al.*, 2002) (Stewart *et al.*, 1997), and generally improved germination success has been reported for various species in *M. viator* nests when compared to matrix soils (Riginos *et al.*, 2005).

The nutrient enrichment and greater water availability on *M. viator* mounds (Midgley and Musil, 1990; Bekker *et al.*, 2016) may be the most important factor responsible for their unique plant communities (as well as accounting for the enhanced plant growth and distinctive plant physiognomy). To test the hypothesis that termite-modified soils can influence differential seed germination and/or seedling performance, reciprocal germination trials of three plant species associated with *M. viator* nests (*Aloe microstigma*, *Pteronia incana*, and *Tylecodon paniculatum*) and three associated with the matrix (*Anginon* sp., *Pteronia paniculatus*, and *Ruschia decurvans*) were conducted in potted trials in an unheated glasshouse to determine whether the different nutrient and soil-water properties between *M. viator* nest and matrix soils have any influence on seedling germination and growth for Karoo plant species showing such clear habitat preferences.

A second *in situ* experiment was conducted by transplanting seedlings of three matrix and three mound plant species (*A. microstigma*, *P. incana*, *P. paniculata* and *T. paniculatus*) into 1) the foreign habitat (experiment), and 2) back into the original habitat (controls) and monitoring subsequent growth and survival over a one year period, in order to determine if seedling development was influenced by habitat-specific soil variables that could explain sharp contrasts between nest and matrix plant community composition.

## 4.2. Materials and methods

### 4.2.1. Glasshouse germination and survival trials in different soil treatments

Three plant species restricted to *M. viator* nests at Worcester (*A. microstigma*, *P. incana*, and *T. paniculata*), and three species only occurring on matrix soils (*Anginon* sp., *P. paniculata*, and *R. decurvans*) were used in the germination trials (Rahlao *et al*. 2008; personal observation). A total of 500 seeds of each species were collected *in situ* in Worcester during autumn (April) of 2017, and several soil samples randomly collected from the matrix were mixed to fill two 25 L buckets. Similarly, soil samples were collected from the first 15 cm of soil off several randomly-selected *M. viator* nests and again mixed to fill two 25 L buckets. These soil samples were pre-prepared by passing them through a 1 mm mesh sieve to remove stones, organic debris and the bulk of larger seeds. A total of 120 pots (7 x 7 x 10 cm) were filled with the soils. Each pot was prepared by placing (±1.5 cm) of drainage stones on top of tissue paper to avoid water-logging. The pots were then labelled and filled with the appropriate soil treatment - generating 60 nest soil and 60 matrix soil replicates. The pots were then saturated with water. The following day (25 May 2017) 25 planting holes (in a 5 x 5 grid, Figure 4.1.a) approximately 1 cm deep (to avoid shallow-planted seeds from washing away or out of place in the grid during overhead watering) was made in the moist soil of each pot with a wooden dowel rod (±7 mm diameter) and one seed placed in each hole. Only a single species were sown in each pot. The grid was used to facilitate the identification of seedlings from target species and the removal of any other germinated seedlings from the soil. The soil was not sterilized, as doing so may have influenced soil nutrient levels and water-holding capacity. This experimental design yielded a total of 20 pots for each of the six plant species, 10 with matrix soil and 10 with nest soil. The 120 pots were randomly placed on a 6 x 20 pot grid in an unheated glasshouse that received natural light (Plant Propagation Unit, H.W. Pearson Building, University of Cape Town) and was rotated at random during the trial (Figure 4.1.b). The experiment was timed to coincide with the natural onset of the winter rains at the study site.

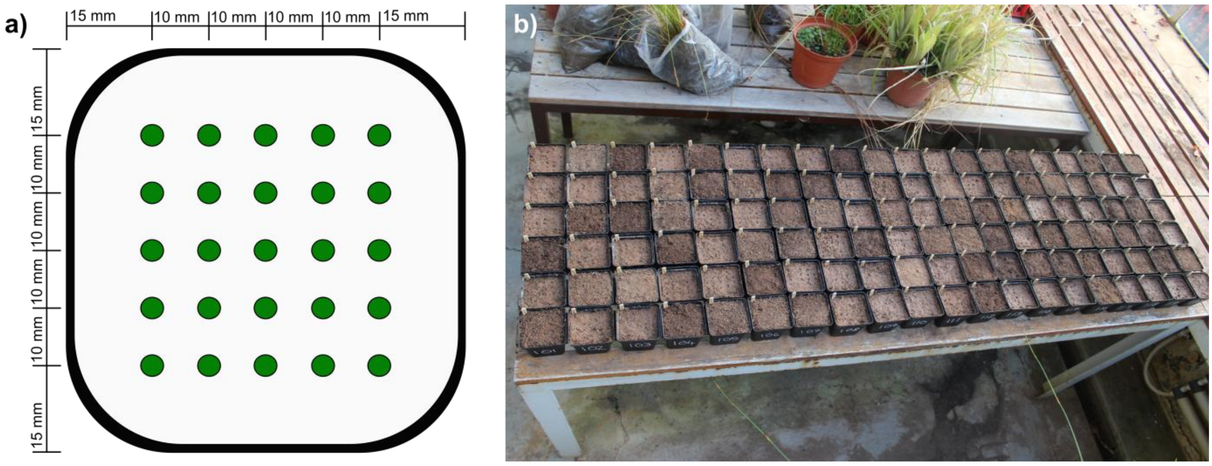

**Figure 4.1.** Experimental design for the greenhouse germination trial; **a)** The grid layout of plant holes (green) for seeds in 7 x 7 cm pots and **b)** The 6 x 20 pot grid in an unheated greenhouse.

All pots were watered (150 ml) daily for the first 65 days to simulate winter rainfall experienced by seeds in natural habitat, thereafter they were watered (250 ml) every other day (Appendix G), simulating drier spring and summer rainfall conditions in the species' natural habitat. The trial was terminated after 162 days, on 2 November 2017. The number of observed germinations (emergence of cotyledons) was recorded once a week per pot (Esler *et al.*, 1992; Esler, 1993), and morphologically dissimilar, opportunistic seedlings from the seed bank that germinated outside the planting grid holes removed. Monitoring of new seedling emergence, along with survival/mortality of each seedling, was continued until the termination of the trial.

### 4.2.2. *In situ* reciprocal transplant experiments at Worcester

In early winter (June 2018) a total of 40 seedlings from each of three *M. viator* nest - associated plant species (*A. microstigma*, *P. incana* and *T. paniculata*) and one matrix (*P. paniculatus*) species, were collected *in situ* at the study site (Worcester). Ideally, two more matrix species would have been preferred for the experiment, however, finding enough suitably-sized seedlings of species associated exclusively or strongly only in the matrix proved impossible, possibly because of the dry conditions over the previous 18 months. The most striking contrast in species cover was between the two *Pteronia* species, each of which had discrete habitat requirements for either mound or matrix. Seedlings were kept cool and damp in a cooler box while baseline root and shoot length (mm), number of leaves (*A. microstigma* and *T. paniculata*) or number of branches (*P. incana* and *P. paniculatus*) were recorded. Following measurements, a seedling of each species was transplanted into

1) each of 20 *M. viator* nest systems, 2) and one into each of 20 matrix plots adjacent (5 m away from *M. viator* nests), and their respective locations recorded (Garmin eTrex Handheld GPS). Thus a single seedling of each species was transplanted into each of the 40 plots. Seedlings (one for each of the four species) were planted in a 20 x 20 cm grid underneath a "*nursery*" bush that would provide some shade during the warmer months (De Villiers *et al.*, 2001; Riginos *et al.*, 2005). For four months (including the winter rainfall period from June to August) seedlings were monitored and given supplementary water (250 ml each) on days with temperatures above 30 °C. Upon termination of the experiment (onset of summer in October 2018), growth performance measurements, as described above, were repeated on the excavated seedlings. In addition, a health score of 1-5 was assigned to each seedling (where 1 = healthy, 2 = surviving, 3 = stressed, 4 = barely alive, 5 = dead), with 0 assigned to missing seedlings (animal interference). Records of 0 were omitted from analyses.

### 4.2.3. Characterisation of soil properties

#### 4.2.3.1. Water infiltration time

After seedlings were transplanted at Worcester, the water infiltration time of nest and matrix soils at the plots were determined by hammering a metal pipe (5 cm diameter) 5 cm into the soil, filling it with 25 ml of water, and recording the elapsed time (seconds) for the water to empty into the soil.

#### 4.2.3.2. Soil nutrients

A soil sample (±1 kg, at a depth of 10-15 cm) was collected from each of the 20 nest and matrix plots to determine the nutrient (C, Ca and N) concentration and other soil variables (mean soil particle size, water holding capacity, and water retention time).

For nutrient analyses, a sub-sample of 100 g from each site was prepared by sieving through a 1 mm mesh, air-dried (24 h), and 50 g of each sub-sample delivered to the Diagnostics Laboratory of the Department of Agriculture, Elsenburg (Stellenbosch) for new, sample-associated nutrient analyses, distinct from those of Chapter 3 (methods as described in Chapter 3).

#### 4.2.3.3. Soil particle size

For mean particle size determination 100 g sub-samples from each site were prepared by sieving the soil through a 1 mm mesh and placing ±0.45 g of the respective sub-sample into an Eppendorf Tube filled to the 20 ml mark with distilled water, and then left overnight to disaggregate the sample. A Malvern Hydro 2000G wet dispersion unit sequentially introduced each prepared sub-sample to the laser diffractometer of a Malvern Mastersizer 2000 (Malvern Instruments Ltd., Malvern, UK) to determine and record soil particle size distributions on the associated software (Wentworth, 1922).

#### 4.2.3.4. Water holding capacity and retention time

The remainder of the original soils were air-dried for 7 days, and prepared for determination of water holding capacity and retention time by first passing samples through a 1 mm sieve. Each sieved sample was used to fill its own pot (7 x 7 x 10 cm), which was weighed to record a baseline dry-soil weight (g). Pots were placed in water-filled trays and left overnight to saturate. The following day, the water-saturated pots were placed on a steel rack (60 min) to drain excess water, and re-weighed to record saturated wet-soil weight (g). The water holding capacity (ml) was calculated by subtracting the dry-soil weight from wet-soil weight. The water-saturated pots were then placed in drying ovens set to 30 °C and left to dry until they once more reached baseline dry-soil weight, and the number of days required to reach this weight recorded and used to calculate soil-water retention time.

### 4.2.4. Statistical analyses

#### 4.2.4.1. Seed germination

The mean percentage of seeds that germinated per pot for each species was calculated. Seedling survival was calculated as a percentage of the total number of germination events for a particular species that survived until the termination of the trial. Mortality was calculated as a percentage difference between the total number of germination events for a particular species and survival. The data were non-normally distributed and a Mann-Whitney U test used to test for a difference between the various performance medians.

#### 4.2.4.2. Transplant experiments at Worcester

Data for growth parameters, survival and their predictor variables (soil parameters) were imported from Excel (Wickham and Bryan, 2017) and the base packages of R Statistic

Software (Version 3.6.1.) used for statistic description. Data were subjected to Levene's test for equal variance, and comparisons of means made using Student t-tests. Scatter plots (Fox *et al.*, 2016) and a correlation matrix (Harrell and Harrell, 2015) were generated to get a sense of variance and correlation between the variables, and correlation measured with Pearson's product-moment correlation. These data were subjected to modelling through multiple linear regressions to explain the observed responses of dependent variables (the difference between final and initial root- and shoot length, number of leaves/branches, and plant health scores) as a function of the differences between independent (explanatory) variables for the two habitats. Data were then reduced by performing Principal Component Analysis on independent variables of mineral concentrations (C, Ca and N) and the soil-water properties (water percolation rate, water retention time, water holding capacity and mean soil particle size) in an attempt to reduce errors within the model. Finally, the residuals of the resulting models were tested for normality and variance to assess the dependability of each model.

The predictive value of two multiple linear regression models was tested for the dependent variables (DV) of each species (measured growth responses) with the independent soil variables; carbon (C), calcium (Ca) and nitrogen concentration (N), water holding capacity (WHC), mean soil particle size (MSPS), water infiltration time (WIT), and water retention time (WRT) for Model 1, and with the reduced soil data variables *NutrientsPC*, *SoilPC1* and *SoilPC2* for Model 2, with the corresponding habitat (H), either *M. viator* nest (0) or matrix (1), and coefficients (m) expressed as:

**Model 1:**

$$DV = m + m(H) + m(C) + m(Ca) + m(N) + m(WHC) + m(MSPS) + m(WIT) + m(WRT)$$

and

**Model 2:**

$$DV = m + m(H) + m(\mathit{NutrientsPC}) + m(\mathit{SoilPC1}) + m(\mathit{SoilPC2})$$

Based on these results additional models were tested using the independent variables identified as significant at a 90 % or higher confidence interval in Models 1 and 2, as well as those with significant correlation with the dependent variables (Appendix H). Including independent variables identified at the 90 % confidence interval, in the absence of/in addition to a model at the 95 % confidence interval, may allow the identification of variables that were not well represented or under-valued in light of the poor performance of transplanted seedlings as a result of interactions between independent variables. Two of the three quantitative model-sets tested for a reduction in root and shoot length, as the mean difference in these variables before and after the experiment for all species was negative (Table 4.5). Models tested the change in the number of leaves, however, would test for growth, as the mean number of leaves increased for all species, except *T. paniculatus,* for which the model will test for leaf reduction. Models that significantly predicted the effect of habitat (H) were then subject to tests for interactions between H and independent variables.

## 4.3. Results

### 4.3.1. Seed germination and survival trials in matrix and *M. viator* nest soils

Germination was generally poor, ranging from 3 - 54 % across all species. Germination of most species was greater in nest than in matrix soils (Appendix I). Germination of *A. microstigma*, *P. incana* and *T. paniculata* in nest and matrix soils followed the expected predicted outcome of higher germination in nest soils based on their natural habitat preference, while this was the opposite for *Anginon* sp., *P. paniculata*, and *R. decurvans,* which were expected to have higher germination in matrix soils. However, only germination of the nest species *P. incana* and *R. decurvans* were higher in nest than matrix soils (Table 4.1) after 162 days. *Anginon* sp. had similar, high levels of germination in both soil types.

**Table 4.1.** The mean germination per pot (10 x *Microhodotermes viator* nest and 10 x matrix soil treatment replicates) for three species associated with nest habitats (green) and three species associated with matrix habitats (orange), and standard deviation (SD), with germination as a percentage of the total number of seeds sown per species ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Mann-Whitney U).

| **Species** | **Mean germination (±SD) per pot/25 seeds** | | **Germination %** | |
|---|---|---|---|---|
| | **Nest** | **Matrix** | **Nest** | **Matrix** |
| ***Aloe microstigma*** | 9.6 (±4.50) | 6.1 (±3.67) | 38.4 | 24.4 |
| ***Pteronia incana*** | 8.4 (±7.01)* | 1.5 (±1.08)* | 33.6 | 6.0 |
| ***Tylecodon paniculata*** | 9.7 (±8.64) | 3.6 (±2.80) | 38.8 | 14.4 |
| ***Anginon* sp.** | 13.5 (±4.67) | 12.4 (±3.66) | 54.0 | 49.6 |
| ***Pteronia paniculatus*** | 8.1 (±9.47) | 2.7 (±2.16) | 32.4 | 10.8 |
| ***Ruschia decruvans*** | 5.6 (±7.89)* | 0.8 (±1.03)* | 22.4 | 3.2 |

There was considerable germination of seeds already present in the collected soil (1209 seedlings in total, viz 10/pot) beyond the grid for the 60 days, but this gradually tapered off after that to a total of 2058 over 162 days (±17 per pot). When monitoring germination, volunteer germination was recorded before carefully removing volunteer seedlings and their developing radicles from the pot. Volunteer seedlings were identified primarily on location in the pot relative to the grid, but also by distinct differences in the cotyledons compared to experimental seedlings which emerged from the grid, indicating that they were a different species

Although mortality of greenhouse seedlings was extremely high following desiccation as a result of missed watering over a few exceptionally hot days, it is worth noting the tolerance observed in seedlings that survived this heat stress in relation to their soil treatments (Table 4.2). Two of the three nest species (*A. microstigma* and *P. incana*) had comparatively greater survival in native nest soils, compared to that of matrix soils (Table 4.2). Seedlings of the third nest species, *T. paniculatus*, however, fared better in matrix soils (10.4 % survival) compared to in nest soils (0.0 %) after the drying period. Comparatively more seedlings of *Anginon* sp. survived in nest (1.6 %) than matrix (0.8 %) soil treatments.

**Table 4.2.** Survival of germinated seedlings after 162 days in the greenhouse following unintended desiccation during extreme greenhouse temperatures in August 2017. Species associated with nests of *Microhodotermes viator* in green, and species associated with matrix habitats in orange ($p < 0.05$ = *****; $p < 0.01$ = ******; $p < 0.001$ = *******; Mann-Whitney U).

| **Species** | **Germinated seedling survival (%)** | |
|---|---|---|
| | **Nest** | **Matrix** |
| ***Aloe microstigma*** | 3.26 | 1.82 |
| ***Pteronia incana*** | 1.6 | 0 |
| ***Tylecodon paniculatus*** | 0 | 10.4 |
| ***Anginon* sp.** | 1.6 | 0.83 |
| ***Pteronia paniculata*** | 0 | 0 |
| ***Ruschia decurvans*** | 0 | 0 |

### 4.3.2. Contrasting properties of matrix and *M. viator* nest soils

Broadly, nest soils were nutrient-enriched and had improved water holding capacity, when compared to matrix soils. All nutrient concentrations measured were significantly higher (carbon $p < 0.01$, calcium and nitrogen $p < 0.001$, Mann-Whitney U) in nest soils, compared to matrix soils (Appendix J). Of the soil properties measured, mean particle size and water infiltration time were higher in matrix than in nest soils, and water holding capacity and retention time were higher in nest than in matrix soils (Table 4.3). However, only water infiltration and retention times differed significantly across the two habitats.

**Table 4.3.** Comparing mean and standard deviation (SD) of nutrient concentrations and measured physical soil properties of *Microhodotermes viator* nest and matrix soils.

| Explanatory variable | Matrix mean (SD) | Nest Mean (SD) | Significance |
|---|---|---|---|
| **Carbon (%)** | 2,60 (±1,11) | 3,88 (±1,85) | * |
| **Calcium (cmol/kg)** | 3,00 (±2,71) | 9,46 (±6,27) | ** |
| **Nitrogen (%)** | 0,16 (±0,05) | 0,25 (±0,10) | ** |
| **Mean particle size (µm)** | 224,05 (±62,56) | 202,76 (±45,07) | ns |
| **Water holding capacity (ml)** | 85,69 (±15,26) | 96,49 (±18,31) | ns |
| **Water infiltration time (sec/ml)** | 511,29 (±442,90) | 135,82 (±137,92) | ** |
| **Retention time (days)** | 11,45 (±4,20) | 14,90 (±5,27) | * |

* = $p < 0.01$; ****** = $p < 0.001$; ns (not significant) $p > 0.05$, Mann-Whitney U

In preparation for a multiple regression model, these independent variables were regressed against the dependent plant growth variables (root and shoot length, number of leaves/branches of transplanted seedlings, and qualitative health score) to identify relationships in preparation for developing a multiple linear regression model (Appendix K). The independent variables were tested for auto-correlation to identify any collinearity (Table 4.4). In the dataset for matrix (blue) independent variables, there was significant ($p < 0.001$), high (79 – 98 %) auto-correlation between carbon, calcium and nitrogen, and water-holding capacity had significant ($p < 0.05$) correlation with mean soil particle size (49 %) and soil water retention time (58 %, $p < 0.05$). There was significant correlation for nitrogen with carbon (90 %, $p < 0.001$) and calcium (47 %, $p < 0.05$) in the dataset for *M. viator* nest (red) independent variables (Table 4.4).

These variables were thus subject to a Principal Component Analysis (PCA) to simplify the complexity of relations between nutrient and soil variables respectively. The resulting Eigenvector *NutrientsPC* was a linear vector combination of carbon, calcium and nitrogen (loading scores: -0.58, -0.55 and -0.60 respectively), which explains up to 90 % of the variation in the measured nutrient data.

**Table 4.4.** Pearson correlation (r) and significance ($p < 0.05$ = *****; $p < 0.01$ = **) matrix of explanatory/independent variables in *Microhodotermes viator* nest (red) and the associated matrix (blue) habitats.

| | | **Carbon** | **Calcium** | **Nitrogen** | **Particle size** | **Water holding capacity** | **Infiltration rate** | **Retention time** |
|---|---|---|---|---|---|---|---|---|
| **Carbon** | **r** | 1 | 0,3989 | **0,8995** | 0,448 | **0,7301** | -0,1736 | 0,3597 |
| | **p-value** | N/A | 0,0907 | **0,0000**** | 0,0544 | **0,0004**** | 0,4773 | 0,1304 |
| **Calcium** | **r** | **0,7861** | 1 | **0,4686** | -0,0535 | **0,5478** | 0,1394 | **0,0464** |
| | **p-value** | **0,0002**** | N/A | **0,043*** | 0,8278 | **0,0152*** | 0,5693 | **0,0456*** |
| **Nitrogen** | **r** | **0,9723** | **0,8237** | 1 | 0,3268 | **0,8001** | -0,1286 | 0,3399 |
| | **p-value** | **0,0000**** | **0,0000**** | N/A | 0,1721 | **0,0000**** | 0,5999 | 0,1545 |
| **Particle size** | **r** | 0,369 | **0,5174** | 0,3199 | 1 | 0,1317 | 0,2838 | 0,4164 |
| | **p-value** | 0,1449 | **0,0334*** | 0,2136 | N/A | 0,591 | 0,239 | 0,0762 |
| **Water holding capacity** | **r** | **0,901** | **0,7449** | **0,8921** | **0,4852** | 1 | -0,2647 | 0,3744 |
| | **p-value** | **0,0000**** | **0,0006**** | **0,0000**** | **0,0483*** | N/A | 0,2735 | 0,1143 |
| **Infiltration rate** | **r** | 0,1406 | 0,325 | 0,1122 | 0,0439 | -0,0534 | 1 | 0,2914 |
| | **p-value** | 0,5904 | 0,2031 | 0,6681 | 0,8671 | 0,8388 | N/A | 0,2262 |
| **Retention time** | **r** | **0,4857** | 0,1901 | **0,4951** | -0,0478 | **0,578** | -0,1315 | 1 |
| | **-value** | **0,0481*** | 0,4649 | **0,0433*** | 0,8555 | **0,0151**** | 0,6149 | N/A |

Principal component analyses of soil properties identified two Eigenvectors (*SoilPC1* and *SoilPC2*) as linear combinations of mean soil particles size, soil water-holding capacity, and water percolation rate and retention time (respective loading scores for *SoilPC1*; 0.29, 0.69, -0.18 and 0.64, and for *SoilPC2*; -0.65. 0.15, -0.74 and -0.08), which together explain a total of 74 % (41 and 33 % respectively) of the variation in the measured soil data.

### 4.3.3. Performance of transplanted seedlings in relation to soil habitat variables

In 2016 and 2017, mean annual precipitation in Worcester (Appendix A) declined after good rain in 2013 and 2014 (476 and 369 mm respectively) to the lowest level for the preceeding 10 years (151 and 169 mm respectively), before starting to recover in 2018 (257 mm), the year of the onset of this experiment. From observations of vegetation at the Worcester site, the impact of these drought years was still evident in 2018, with much of the local shrubby vegetation dead, or showing partial dieback, especially of mature *Pteronia* spp. The drought conditions also likely impacted the survival of seedlings in the reciprocal field transplant experiment, despite provisions made for additional watering on extremely warm days. Under normal conditions, control species transplants into native soil habitats would likely not have had such great mortality as that observed under stressed conditions of the drought and unusually warm winter temperatures in 2018.

Plant vigour generally decreased across all species for the duration of the experiment (Appendix L). However, only *P. paniculata* seedlings had a significant ($p < 0.05$, Mann-Whitney U) difference in mean qualitative health score between the two habitats, being healthier in nest soils. None of the differences in measured performance variables for plant growth was significant between the two field habitats for any of the species investigated (Table 4.5). The mean root and shoot lengths of all species were reduced compared to initial measurements, irrespective of field habitat. The mean root lengths of *A. microstigma*, *P. incana* and *T. paniculatus* had a slightly greater reduction in matrix than nest soils, and *P. paniculata* root length was more reduced in nest than in matrix soils. The mean shoot lengths of *P. incana* and *T. paniculatus* were more reduced in matrix than nest soils, whereas those of *A. microstigma* and *P. paniculata* were more reduced in nest soils. The mean number of *A. microstigma* leaves increased in both matrix and nest soil habitats, however this increase was slightly greater in matrix soils. The mean number of leaves on *T. paniculata* seedlings, however, decreased in nest soils and increased in matrix soils. The number of *P. incana* branches increased more in nest than matrix soil treatments, whereas that of *P. paniculata* increased more in matrix than nest soil treatments. The mean qualitative health score of matrix species indicated that *A. microstigma*, *P. incana* and *T. paniculatus* were all slightly healthier after being transplanted in matrix soil, compared to counterparts planted in nest soil.

**Table 4.5.** The mean change and standard deviation (±) of response variables (number of leaves/branches, root length, and shoot length) of plant species in each habitat (*Microhodotermes viator* nest and matrix) as well as the mean qualitative health score. The unequal sample sizes due to loss of samples to wildlife disturbance are indicated (Nest n and Matrix n).

| Species | Variable | Nest | Matrix | Significance |
|---|---|---|---|---|
| ***Aloe microstigma***<br>(Nest n = 16,<br>Matrix n = 20) | **Root length** | -25,19 (±49,91) | -25,55 (±32,41) | ns |
| | **Shoot length** | -18,06 (±14,25) | -8,89 (±27,16) | ns |
| | **Number of leaves** | 0,50 (±1,10) | 1,00 (±1,86) | ns |
| | **Health score** | 1,44 (±1,03) | 1,55 (±0,95) | ns |
| ***Pteronia incana***<br>(Nest n = 17,<br>Matrix n = 19) | **Root length** | -29,77 (±64,01) | -30,16 (±55,26) | ns |
| | **Shoot length** | -32,72 (±40,83) | -38,19 (±46,00) | ns |
| | **Number of branches** | 3,00 (±9,77) | 0,90 (±6,05) | ns |
| | **Health score** | 3,53 (±1,74) | 3,74 (±1,91) | ns |
| ***Pteronia paniculata***<br>(Nest n = 17,<br>Matrix n = 19) | **Root length** | -20,53 (±28,96) | -8,16 (±43,10) | ns |
| | **Shoot length** | -41,46 (±32,84) | -31,30 (±26,72) | ns |
| | **Number of branches** | 2,59 (±4,96) | 4,11 (±9,07) | ns |
| | **Health score** | 4,59 (±0,80) | 3,58 (±1,54) | * |
| ***Tylecodon paniculatus***<br>(Nest n = 17,<br>Matrix n = 18) | **Root length** | -12,56 (±15,60) | -12,71 (±17,16) | ns |
| | **Shoot length** | -18,15 (±17,91) | -22,16 (±20,10) | ns |
| | **Number of leaves** | -1,06 (±1,89) | -0,83 (±2,48) | ns |
| | **Health score** | 2,88 (±1,87) | 3,06 (±1,55) | ns |

($p < 0.05$ = *****; ns (not significant) $p > 0.05$, Mann-Whitney U and Student T-test)

The measured reduction of dependent variables (root and shoot length, and the number of leaves/branches) can be attributed to *planting check* (transplant shock) (South and Zwolinski, 1997), which is defined as a period after being transplanted when seedlings are susceptible to stress, injury, mortality and reduced growth in response to physical handling and change in soil and environmental conditions (Hobbs, 1992; Haase and Rose, 1993; Close *et al.*, 2005). Only the survival of *Pteronia* spp. seedlings conformed to the expectation of greater survival in their native soils (Table 4.6); *P. incana* having greater survival in nest soils, and *P. paniculata* having greater survival in matrix soils.

**Table 4.6.** The percentage of seedlings that survived (qualitative health score 1 – 4) the reciprocal transplant experiment in *M. viator* nest and the associated matrix habitats.

| Species | Nest survival (%) | Matrix survival (%) |
|---|---|---|
| *Aloe microstigma* | 80 | 90 |
| *Pteronia incana* | 50 | 30 |
| *Pteronia paniculata* | 20 | 60 |
| *Tylecodon paniculatus* | 50 | 60 |

### 4.3.4. Explaining plant growth as a function of soil variables

#### 4.3.4.1. Assessing variables of multiple linear regression models for *Aloe microstigma* performance

The only significant correlation of dependent growth variables with independent variables of *A. microstigma* was for qualitative health score with water infiltration time (39 %, $p < 0.05$), it is thus expected that health will improve along with an increase in water infiltration rate. Water infiltration rate was significantly lower in nest than matrix habitats (Table 4.3), however, no significant difference was found in health score for *A. microstigma* between the two habitats (Table 4.5). There was an additional significant ($p < 0.01$), moderate (52 %) correlation between two dependent variables; shoot length and number of leaves. This was not surprising, as shoot length of *A. microstigma* was measured as the length of above-ground parts, which in this species consists primarily of leaves. The strongest correlating (though not significant) independent variable with reduction in root length was Ca concentration (25 %, $p = 0.14$); with reduction in shoot length was N concentration (17 %, $p = 0.33$); and with number of leaves was N concentration (32 %, $p = 0.06$).

Several models were tested for the effect of habitat (H) on root reduction of *A. microstigma* (Appendix H). When controlling for the concentrations of C, Ca and N, and mean soil particle size, water holding capacity, infiltration/percolation rate, and retention time, there was a significant main effect of H ($p < 0.05$), with a standard error (SE) of 34.32 and 27 degrees of freedom (df), which had a significant ($p < 0.01$) interaction with and depends on WIT. The recommended model (**AMR**) to determine the effect of habitat on root reduction of *A. microstigma* and explaining 45 % of the observed variation was thus:

**AMR** (SE = 34.32; df = 27):

$$\text{Root length (mm)} = 9.14 - 48.18(\text{H}) + 27.81(\text{C}) - 6.86(\text{Ca}) - 224.49(\text{N}) - 0.26(\text{MSPS}) + 0.58(\text{WHC}) + 0.07(\text{WIT}) - 2.43(\text{WRT})$$

Two models that identified significant ($p < 0.05$) effect by habitat on the number of leaves gained by *A. microstigma* were produced. The first model (**AML1**) included the controlled data variables *NutrientsPC*, *SoilPC1* and *SoilPC2*, while the second model (**AML2**) omitted independent variable *SoilPC1,* which was found to be non-significant in AML1. No significant interaction of H could be found in either model with any of the independent variables. The two models recommended to predict leaf gain of *A. microstigma*, explaining 26 and 24 % of the observed variation, respectively, are:

**AML1** (SE = 1.44; df = 31):

Leaf growth = 0.02 + 1.44(H) – 0.61(*NutrientsPC*) – 0.24(*SoilPC1*) + 0.44(*SoilPC2*)

**AML2** (SE = 1.43; df = 32):

Leaf growth = 0.03 + 1.41(H) – 0.47(*NutrientsPC*) + 0.47(*SoilPC2*)

No models were found to significantly predict the reduction in shoot length, or qualitative health of *A. microstigma* in response to habitat. A summary of the tests for these models, and additional tests for other models predicting the reduction in root length, and the number of leaves, omitting non-significant independent variables and which were not significant are summarized in Appendix H.

#### 4.3.4.2. Assessing variables of multiple linear regression models for *Pteronia incana* performance

Reduction in *P. incana* root length was significantly (35 %, $p < 0.05$) correlated with C concentration (Appendix L). The C concentration was significantly ($p < 0.01$) greater in nest than matrix habitats (Table 4.3), however, no significant difference was found in the reduction of *P. incana* root length between the two habitats (Table 4.5). In addition, there was a significant correlation of reduction in root length with that of the number of branches (48 %, $p < 0.01$) and qualitative health (58 %, $p < 0.001$), as well as between reduction in shoot length and the number of branches (77 %, $p < 0.001$). The strongest correlating (though not significant) independent variable with reduction in shoot length was water retention time (20 %, $p = 0.26$); with number of branches was Ca concentration (32 %, $p = 0.06$); and with qualitative health was C concentration (26 %, $p = 0.13$).

None of the models tested to investigate the effect of H on dependent variables of *P incana* was significant at the 95 % confidence level. However, two models were significant at the 90 % confidence level; they were the reduction in root (**PIR**) and shoot length (**PIS**), explaining 13 and 15 % of the observed variation, respectively. Neither of these models found any significant interaction of H with any other independent variables.

**PIR** (SE = 56.33, df = 33):

Root reduction (mm) = -42.42 + 23.59(H) – 14.93(*NutrientsPC*)

**PIS** (SE = 40.81, df = 32):

Shoot reduction (mm) = 49.16 + 11.27(H) + 340.00(N) – 1.92(WHC)

#### 4.3.4.3. Assessing variables of multiple linear regression models for *Pteronia paniculata* performance

The reduction of root length for *P. paniculata* was significantly (41 %, $p < 0.05$) correlated with water infiltration/percolation rate (Appendix L). Matrix habitats had a significantly ($p < 0.001$) greater WIT (Table 4.3), and thus it was expected that the reduction in root length would greater in matrix than nest habitats, however, no significant difference was found between root reduction of *P. paniculata* between these habitats (Table 4.5). Reduction of shoot length was significantly correlated with other dependent variables number of branches (51 %, $p < 0.01$) and qualitative health (-37 %, $p < 0.05$). The strongest correlating (though not significant) independent variable with reduction in shoot length and number of branches was WHC (32 %, $p = 0.06$; 19 %, $p = 0.27$, respectively); and with qualitative health was Ca concentration (19 %, $p = 0.26$).

Models were developed that significantly explained the effects of habitat for *P. paniculata* reduction in root and qualitative health score. The model for the effect of habitat on reduction in root length (**PPR**, $p < 0.05$) was developed by omitting non-significant independent variables from base model 1, explaining 17 % of the observed variation in root length reduction of *P. paniculata*.

**PPR** (SE = 34.81,df = 33):

Root reduction (mm) = $-25.11 - 6.23(H) + 0.04(WIT)$

Two models were developed to investigate the effect of H on qualitative health of *P. paniculata*. The first model (**PPH1**, $p < 0.01$) was developed by omitting non-significant independent variables from base model 1, while the next model (**PPH2**, $p < 0.05$) included all reduced independent variables. Both models explained 33 % of the observed variation in qualitative health of *P. paniculata*.

**PPH1** (SE = 1.12, df = 33):

Health score $= 4.99 - 1.77(H) + 0.01(\mathit{NutrientsPC}) - 1.7(\mathit{SoilPC1}) - 0.56(\mathit{SoilPC2})$

**PPH2** (SE = 1.16, df = 31):

Health score $= 4.40 - 1.77(H) + 0.002(WIT)$

Base model 2 (including only reduced independent variables) for reduction in shoot length of *P. paniculata* was found to be significant at the 90 % confidence interval.

#### 4.3.4.4. Assessing variables of multiple linear regression models for *Tylecodon paniculatus* performance

None of the dependent growth variables of *T. paniculatus* had any significant correlation with any of the measured dependent variables (Appendix L). However, among dependent variables, the reduction in root length had significant correlation with the reduction in shoot length (63 %, $p < 0.001$), loss of leaves (41 %, $p < 0.05$) and qualitative health (-51 %, $p < 0.01$). In addition, reduction in shoot length had significant correlation with loss of leaves (64 %, $p < 0.001$) and qualitative health (-77 %, $p < 0.001$), the latter of which was also significantly (-82 %, $p < 0.001$) correlated with loss of leaves. The strongest correlating (though not significant) independent variable with reduction in root length was N concentration (-32 %, $p = 0.06$); with reduction in shoot length was Ca concentration (16 %, $p = 0.35$); with loss of leaves was mean soil particle size (30 %, $p = 0.08$); and with qualitative health was also mean soil particle size (31 %, $p = 0.07$). The only significant ($p < 0.05$) model developed for the effect of H on *T. paniculatus* was for the loss of leaves (**TPL**) which included all independent variables and explained 42 % of the observed variation.

**TPL** (SE = 1.90, df = 26):

$$\text{Leaf loss} = 0.15 + 1.49(H) + 0.58(C) + 0.32(Ca) - 26.22(N) + 0.02(MSPS) - 0.06(WHC) - 0.003(WIT) + 0.24(WRT)$$

A model was developed for root reduction of *T. paniculatus* that was only significant to the 90 % confidence interval by omitting all non-significant independent variables from base model 1, leaving only H and N in the equation. Subsequent tests found that the effect of H is dependent on N concentration at the 90 % confidence level. A summary of the variable intercepts for significant growth/reduction models for all species (*A. microstigma*, *P. incana*, *P. paniculata*, and *T. paniculatus*) is provided in Table 4.7.

**Table 4.7.** Significant growth/reduction models for *Aloe microstigma* roots (AMR) and number of leaves (AML1 and AML2), *Pteronia incana* roots (PIR) and shoots (PIS), *P. paniculata* roots (PPR) and health (PPH1 and PPH2), and *Tylecodon paniculatus* number of leaves (TPL) and their intercept values (C – Carbon; Cal – Calcium; N – Nitrogen; MSPS – Mean Soil Particle Size; WHC – Water Holding Capacity; WIT – Water Infiltration Time; WRT – Water Retention Time; NutrientsPC – reduced data of C, CA and N; SoilPC1 – reduced data of MSPS and WHC; SoilPC2 – reduced data of WIT and WRT).

| Variable | AMR (SE = 34,32; df = 27) | AML1 (SE = 1,44; df = 31) | AML2 (SE = 1,43; df = 32) | PIR (SE = 56,33; df = 33) | PIS (SE = 40,81; df = 32) |
|---|---|---|---|---|---|
| **Intercept** | 9,14 | 0,02 | 0,03 | -42,42 | 49,16 |
| **Habitat** | -48,18 | 1,44 | 1,41 | 23,59 | 11,27 |
| **C** | 27,81 | - | - | - | - |
| **Ca** | -6,86 | - | - | - | - |
| **N** | -224,49 | - | - | - | 340,00 |
| **MSPS** | -0,26 | - | - | - | - |
| **WHC** | 0,58 | - | - | - | -1,92 |
| **WIT** | 0,07 | - | - | - | - |
| **WRT** | -2,43 | - | - | - | - |
| **NutrientsPC** | - | -0,61 | -0,47 | -14,93 | - |
| **SoilPC1** | - | -0,24 | - | - | - |
| **SoilPC2** | - | 0,44 | 0,47 | - | - |

| | PPR (SE = 34,81; df = 33) | PPH1 (SE = 1,12; df = 33) | PPH2 (SE = 1,16; df = 31) | TPL (SE = 1,90; df = 26) |
|---|---|---|---|---|
| **Intercept** | -25,11 | 4,99 | 4,40 | 0,15 |
| **Habitat** | -6,23 | -1,77 | -1,77 | 1,49 |
| **C** | - | - | - | 0,58 |
| **Ca** | - | - | - | 0,32 |
| **N** | - | - | - | -26,22 |
| **MSPS** | - | - | - | 0,02 |
| **WHC** | - | - | - | -0,06 |
| **WIT** | 0,04 | - | 0,002 | -0,003 |
| **WRT** | - | - | - | 0,24 |
| **NutrientsPC** | - | 0,01 | - | - |
| **SoilPC1** | - | -1,70 | - | - |
| **SoilPC2** | - | -0,56 | - | - |

## 4.4. Discussion

### 4.4.1. Glasshouse germination and survival trials in different soil treatments

The two species of *Pteronia,* which are amongst the most abundant species at the study site, provided an ideal test for how localised soil gradients can influence community composition with *P. incana* - restricted to nest sites, and *P. paniculata* growing in the matrix. Higher germination under greenhouse conditions was found for nest-native *P. incana* and *R. decurvans* in nests soils (Table 4.1), while greater survival of germinated matrix-native *P. incana* in nest soils following heat and water stress indicated greater tolerance in native nests soils (Table 4.2).

For the field trials *health scores* of matrix-native *P. paniculata* were greater for nest than matrix habitats. Although the latter difference was contrary to what was expected, the differences in root and shoot reduction and the number of branches for *P. incana* and *P. paniculata* followed the expected outcomes, despite these differences not being significant (Table 4.5). Both germination success and vigour of transplanted seedlings thus provided evidence that both factors are important in determining community composition of this genus at Worcester. If soil type influenced germination success, nest species (*A. microstigma*, *P. incana*, and *T. paniculatus*) might be expected to have significantly higher germination success in their native nest soils than in foreign matrix soils, and the same would be true for matrix species (*Anginon* sp. *P. paniculata* and *R. decurvans*) in their native matrix soils.

Seeds of *P. incana* had significantly greater germination success in soil treatments from their native nest habitat, compared to that of the matrix habitat (Table 4.1). However, all species, including those native to matrix soils, had a greater germination success in nest soil treatments compared to matrix soil treatments, but only that of *P. incana* and *R. decurvans* was significant. It is possible the higher germination of *A. microstigma* and *T. paniculatus* in nest than in matrix soils could have been significant, had the sample size been larger, given the generally low germination success. *Aloe* seeds usually germinate within 21 days of dispersal, although species in drier regions may remain viable for up to three years (Cousins and Witkowski, 2012). Since *A. microstigma* falls in the latter category, it is possible that an extended trial would have resulted in greater germination success in either or both of the treatments. According to the South African National Biodiversity Institute (SANBI), *T. paniculatus* seeds readily germinate during cold autumn temperatures (within 10 – 30 days) and grow incredibly slowly (±2.5 cm during the first year). A refinement of the conditions used in the germination experiments would be that the fine seeds be sown on top of a coarse sand substrate (Oliver and Reynolds, 2002). It is thus unlikely any further germination of *T. paniculatus* seeds would have occurred had the trial been extended. The seeds sowed ± 1 cm in the substrate were covered with soils taken from the field to ensure seeds were not washed away or moved during irrigation of the pots. Although some seeds did germinate within the assigned grid, it is possible that seeds were sown too deep for effective germination. A comprehensive review on dormancy and germination syndromes for Karoo plant species (Van Rooyen and De Villiers, 2004) described seed dormancy factors (light, temperature, endogenous rhythms, chemical signals, and water-soluble germination inhibitors). Light detection in seeds may be necessary for germination, preventing germination of especially small seeds buried too deep to emerge successfully. In some species, photosensitive reactions occur at different temperature thresholds which also may have been too high under greenhouse conditions for some seeds to germinate (Henrici, 1935; Henrici, 1939).

It was expected that germination of *Anginon* sp., *P. paniculata*, and *R. decurvans* would have been significantly higher in their observed native matrix soils (Rahlao *et al.*, 2008), compared to foreign nest soils. However, subsequent visits to the site revealed scattered populations of *Anginon* on nests, as well as in the matrix, excluding it as a genuine matrix-restricted species. In any case, there was little difference in germination success in both soil types. In germination trials there was no significant difference in germination success in either soil type for *P. paniculata*, which has previously been noted to have poor germination success (Rahlao *et al.*, 2008). Germination success of *R. decurvans*, in contrast to what was expected, was significantly higher in nest soils compared to matrix soils. In transplant experiments, seedlings of other Karoo species were reported to have better performance (measured as survival) on nest than in the matrix soils, despite their native soil habitats (nest or matrix), attributed to more favourable nutrient and soil-water conditions (Midgley and Musil, 1990; Riginos *et al.*, 2005).

Under field conditions, subsequent to germination other factors (competition, post seedling growth, etc) might influence survival to generate the community pattern where *R. decurvans* is largely restricted to the matrix plant community. It appears that at least part of the mechanism of habitat selection in *A. microstigma* and *P. incana* is active during seedling growth in the form of improved tolerance to unfavourable conditions (desiccation following missed watering schedule and high glasshouse temperatures). Tolerance of abiotic stress, particularly drought stress, has been found to be regulated by K (Hasanuzzaman *et al.*, 2018), a plant nutrient present in abundance on *M. viator* nests compared to the associated matrix (Midgley and Musil, 1990). If certain species are better able to obtain and utilize these higher concentrations of K during times of abiotic stress, it could provide a competitive advantage to displace or out-compete other species that are less able to tolerate stress. This might explain greater survival of *A. microstigma* and *P. incana* in their native nest soil (Table 4.2). *Anginon* sp. which was found to be present in both habitats also had greater survival in nest habitats.

### 4.4.2. Role of soil variables in explaining plant community composition

The elevated nutrient (C, Ca and N) concentrations, improved water retention time (WRT), and water holding capacity (WHC) of nest soils (Midgley and Musil, 1990; Milton and Dean, 1990; Lovegrove, 1991) were expected to be higher than that of the associated matrix, and the mean soil particle size (MSPS), and water infiltration time (WIT) significantly lower on nest soils due to the tunneling and behaviour of termites in active particle selection (termites transporting larger particles to the surface, generating finer-particulate soils) when compared to the associated matrix soils (Dean and Yeaton, 1992; Léonard and Rajot, 2001; Jouquet *et al.*, 2002; Abe *et al.*, 2012). These differences were all found, however, were not significant for MSPS and WHC (Table 4.3).

The growth of the nest plants *A. microstigma*, *P. incana*, *P. paniculata* and *T, paniculatus* was expected to be higher for transplants to their native habitats. Except for increases in the number of leaves/branches (though not significant) for *A. microstigma* and the two *Pteronia* spp., all other growth variables were reduced after the experiment, indicative of transplant stress exacerbated by the drought conditions, and necessitating frequent supplementary watering. The greater increase in the number of leaves for *A. microstigma* in the matrix indicated a contrary trend to what was expected for this nest species. The two *Pteronia* spp., however, had a site-specific increase in the number of branches, consistent with what was expected in terms of their habitat distribution, with *P. incana* having a greater increase in nest (native habitat) than matrix soils, and *P. paniculata* having a greater increase in matrix (its native habitat) than nest soils. The models predicting reduction in *P. incana* (PIR) and *P. paniculata* (PPR) root length which included variables NutrientsPC and WIT found that the variable "*habitat*" best explained this reduction. This reflected what was suspected; that the reduction of *P. incana* root length was greater in foreign matrix habitats, and the reduction of *P. paniculata* root length was greater in foreign nest habitats.

Reduction of shoot length of *P. incana* (PIS) was best explained by a combination of habitat, N concentration in soil, and WHC. The reduction in root length of *A. microstigma* (AMR) and loss of leaves by *T. paniculatus* (TPL) were both best explained by habitat through a combination of all the measured independent variables (Ca, C and N concentration, MSPS, WHC, WIT and WRT), while the number of leaves gained by *A. microstigma* was best explained by habitat in a combination of *NutrientsPC*, *SoilPC1* and *SoilPC2* (AML1), or just *NutrientsPC* and *SoilPC2* (AML2).

Literature on the species-specific effects of transplant on physiology of plant organs such as that above is, to date, restricted to research on transplant shock discussed below. However, transplant experiments previously conducted in the Succulent Karoo explored conditional competitive and facilitative plant-plant interactions between seedlings and adults (Riginos *et al.*, 2005), and reciprocal transplant between the Succulent Karoo and Fynbos to explore selective pressures for these communities (Esler *et al.*, 2015). The former concluded that interactions between adult plants and seedlings are determined by a complex model including variables such as soil nutrients and rainfall. Esler *et al*. (2015) found that Fynbos species are constrained by climate and soil conditions, whereas Succulent Karoo species were better able to exploit a wider range of conditions but were competitively excluded from the Fynbos. This supports the idea of a complex model affecting local distribution of plants.

The duration of transplant shock (as observed in the field experiment) can vary, based on local climatic and possibly soil differences, as demonstrated in spruce (*Picea* spp.) in British Columbia (Vyse, 1981) where it lasted one year, compared to the same species in Ontario, where it lasted between 10-15 years (Mullin, 1963). Comparative literature on growth forms other than long-lived woody trees/shrubs species is lacking. Ideally, seedlings used for transplant experiments are typically produced in bulk in greenhouses to ensure consistent age and significantly high numbers of surviving replicates from a single cohort which can be hardened to have increased tolerance, which would enable them to survive the transplant into field conditions (Liptay *et al.*, 1998). For example, a study investigating the influence of climate and soil on biome boundary using a reciprocal transplant method between the Fynbos and Succulent Karoo biomes (Esler *et al.*, 2015) germinated field-collected seeds in a greenhouse, where they were left to grow for two months, with daily watering after germinating. Following this period, seedlings were moved into direct sunlight and gradually received less water (twice weekly) to harden seedlings for the transplant into field containers (Esler *et al.*, 2015). However, even transplanted seedlings that have been hardened to drought conditions may suffer to some degree from reduced terminal growth and increased mortality, compared to undisturbed controls (Kaushal and Aussenac, 1989; Haase and Rose, 1993). In this study, three of the target species were highly succulent, theoretically reducing their susceptibility to water stress.

The models generated using soil treatment as a variable were able to significantly predict the outcome of several dependent variables for different species. The proposed models for root and shoot growth were associated with negative growth data for all species, and the number of leaves for *T. paniculatus* was reduced in both soil treatments. For this reason, models proposed for the reduction in root and shoot length and the reduction in the number of leaves for *T. paniculatus* could instead be interpreted as models predicting tolerance to transplant shock, rather than growth. The number of leaves for *T. paniculatus* was also reduced, however, this was because this species is a summer deciduous, losing all its leaves in October, which are then regrown in March/April the following year (Van Jaarsveld and Koutnik 2004). The experiment was terminated in October, possibly coinciding with annual leaf abscission.

The observed difference (non-significant) in the reduction of root length for *A. microstigma* in different soil treatments, as predicted by the model (AMR) conform to the expectation that seedling roots are better able to tolerate transplant shock in their native soil habitats. This is possibly because *A. microstigma* is better adapted generally to their native nest soil habitats, and that differential survival might generate the habitat-specific pattern for this species. Models predicting the number of leaves gained by *A. microstigma* (AML1 and AML2) confirmed that soil nutrients significantly influenced model outcomes, which was that seedlings transplanted in matrix soils gained significantly more leaves than those transplanted in nest soils.  This could be explained physiologically by the potentially higher foliar nutrient concentration (Midgley and Musil, 1990; Bonachela *et al.*, 2015) of *A. microstigma* seedlings harvested from nest soils. Following transplantation back into nest soils (which are more enriched and have improved soil-water properties than matrix soils), roots could draw from and replenish nutrient stocks more efficiently, and therefore better tolerate transplant shock in the roots. Seedlings transplanted in matrix soils that could not replenish nutrient stocks as efficiently from the roots, possibly redirected nutrient stocks into leaf production to optimize photosynthesis and N fixation, which would ultimately stabilize the roots (Close *et al.*, 2005).

The models developed to predict transplant shock tolerance in roots and shoots of nest species *P. incana* indicate that roots and shoots of seedlings in nest soil treatments were more tolerant of transplant shock than those in matrix soil treatments. The higher tolerance in nest soil treatments can be attributed to a reduced cost of adaptation, being transplanted into its native soil type, with the observed symptoms of transplant shock attributable to seedlings not being primed for transplant (having been excavated and transplanted in the field) (Vyse, 1981; Close *et al.*, 2005). This suggests that soil type of nest species may play a role in determining fine-grained habitat selection.

For both *P. paniculata* root and shoot length variables, the models were able to significantly predict transplant shock tolerance. Both roots and shoots were able to better tolerate transplant shock in their native matrix soil treatment than in the foreign nest soil treatment for *P. paniculata*. Similar to that observed for *P. incana* in nest soils, these results for *P. paniculata* can possibly be attributed to the reduced cost for adaptation to the native (matrix) soil, as opposed to that of foreign (nest) soil conditions (Vyse, 1981; Close *et al.*, 2005). This was confirmed by the model PPH2 which predicted significantly better health score in native matrix habitat compared to foreign nest habitats.

The model for predicting transplant shock in *T. paniculatus* roots was able to significantly predict 100 % of the smaller reduction in root length (reduced stress) for seedlings in nest habitats compared to matrix habitats, where the cost of adaptation may be lower in transplants to native nest compared to foreign matrix soil treatments. The model produced to predict leaf loss for *T. paniculatus*, despite being able to significantly predict most of the observed leaf losses in nest and matrix habitats, is not a true reflection of tolerance, but of annual leaf abscission. Correlations with measured independent variables could be the result of the physiological processes inducing leaf abscission e.g. changes in water potential that inhibit transport of auxin (Davenport *et al.*, 1977; Hopkins and Hüner, 2004), or else are coincidental.

## 4.5. Conclusion

The results presented here indicate that differential germination success and especially seedling survival as a function of soil type is a possible mechanism for the observed habitat specificity of certain karoo plant species. However, the only species for which the germination trials had the expected outcome was *P. incana,* which had higher germination success and survival in native (nest) rather than foreign (matrix) soil treatments. However, the germination success of other study species did not clearly follow the same prediction e.g. *R. decurvans* had greater germination in foreign nest than native matrix soil treatment the relatively low germination obtained across the study may be related to seed viability or issues related to irrigation of the potted seeds.

Reciprocal transplant experiments to demonstrate differential species selection across different soil treatments found that seedlings of *P. paniculata* had higher qualitative health in native (matrix) soils than those in foreign nest soils. Most of the dependent variables measured, however, were subject to transplant shock limiting the investigation of any improved growth on native versus foreign soils. Instead, it is proposed that seedlings would have a higher tolerance (smaller reduction in the measured variable) to transplant shock in native than foreign soils. The subsequent models suggest differential responses to transplant shock for different dependent variables. The roots of all species showed higher tolerance to transplant in native than foreign soil treatment, suggestive of local adaptation to fine-scale soil differences. Shoots and leaves of *A. microstigma*, leaves of *T. paniculatus*, and branches of *P. paniculata,* however, had higher tolerance in foreign than native soils. The cumulative significant results of objective data (root and shoot length, and number of leaves or branches) demonstrated a higher tolerance to transplant shock in native soils, which had lower adaptation costs, compared with foreign soils, which had higher adaptation costs.

Future research could refine the germination conditions and include a much larger sample size for germination and survival trails of a similar design with larger replicates (and more seeds per species). Heat sterilization of soils prior to germination trials would eliminate seed bank germinations, but this might affect combustible soil C (Neff *et al.*, 2005). It is recommended that the duration for such trials start early in the germination season and continue until the end of the second growing season in a climate-controlled greenhouse. This would allow seedlings to mature and be more tolerant of transplant from germination trays into individual pots. Transplant shock recovery should be monitored and managed, as described by Rietveld (1989) until seedlings have 1) recovered from injury and/stress of being handled, 2) do not show signs of water stress, 3) resume normal growth and respiration, and 4) adapt to the new conditions (Rietveld, 1989; Hobbs, 1992). Mature seedlings that have adapted successfully to individual pots must then be gradually hardened with exposure to natural conditions before being left to grow under natural conditions in the field and monitored over an extended period, depending on known growth rates. The extreme drought conditions (reflected in a paucity of field seedlings to use for the experiment) no doubt contributed to the transplant stress and were unavoidable given the time frame of the study. It is apparent that the mechanisms that determine plant community composition of *M. viator* nests and their associated matrices are complex, but are linked to soil properties. Additional factors e.g. different growth rates, plant-plant interactions and life history and germination strategies (Milton, 1994; Esler and Cowling, 1995; De Villiers *et al.*, 2002; Oliver and Reynolds, 2002; Riginos *et al.*, 2005; Esler *et al.*, 2015) may also play some role in determining habitat selection and thus community composition. What was clear from this study was that soil nutrients and physical properties affecting soil-water conditions as a function of habitat play a significant role in determining plant resilience.

# CHAPTER 5 – *MICROHODOTERMES VIATOR* DRIVES SHARP GRADIENTS IN FLORAL AND FAUNAL COMMUNITIES

## 5.1. Introduction

Termite nests, through their construction and maintenance by termites, create unique niches (Fleming and Loveridge, 2003; Beaudrot *et al.*, 2011; Joseph *et al.*, 2013; Bignell, 2019). Physical and chemical changes to soils (Lee and Wood, 1971b; Erpenbach *et al.*, 2017) associated with termite nests allow improved plant growth and competitive exclusion and selection of plant species on termite nests compared to their associated matrices (examples discussed in Chapters 3 and 4). These unique niches then attract fauna as improved grazing sites (Smith and Yeaton, 1998; Holdo and McDowell, 2004; Seymour *et al.*, 2014), refugia (Pomeroy and Service, 1986; Moreira *et al.*, 2009; Simioni *et al.*, 2014) or hunting grounds (Louw *et al.*, 2017; Henschel and Lubin, 2018) affecting local plant and animal species richness, diversity, and community structure (McAuliffe *et al.*, 2019).

### 5.1.1. Change in plant communities in response to termite nests

Termite nests often harbour plant species and/or growth forms in different frequencies than, or that are absent in the associated matrix. Consequently, termite nests often have distinct plant communities compared to that of the associated matrix vegetation. Plant species richness of *Macrotermes* spp. nests were compared with that of their associated matrices at five savanna sites in Burkina Faso and Benin (Erpenbach *et al.*, 2013). There was no difference in overall mean species richness between nests and matrices. However, when sites were considered separately the two wetter (MAP > 800 mm), southern sites in Benin had a greater species richness associated with termite nests than the associated matrices. This was attributed to differences in soil parameters as a result of termite activity, in addition to increased precipitation. Also, mounds of *Cubitermes* spp., *Microtermes* spp., *Trinervitermes geminatus*, *T. trinervius*, and *Macrotermes bellicosus* in Benin had greater plant species richness than their associated matrices, which correlated with deeper soils associated with termite mounds (Padonou *et al.*, 2020). At both Soebatsfotein and Springbok in South Africa, the Succulent Karoo matrices had greater plant species richness than the associated nests of *Microhodotermes viator* (Kunz *et al.*, 2012; Schmiedel *et al.*, 2016), in both these studies plant richness was correlated with the difference in pH between mounds and matrices.

In Burkina Faso nests of *Macrotermes subhyalinus* harboured plant species (*Tamarindus indica*, *Boscia senegalensis*, *Cadaba farinose*, *Capparis sepiaria* and *Maeruo angolensis*) which were absent in the associated savanna matrix (Traoré *et al.*, 2008). Similarly, nests of *Macrotermes herus* in Uganda also harboured plant species (*Grewia* spp. and *Euphorbia candelabrum*) which were absent in the associated savanna matrix (Moe *et al.*, 2009). In addition nests of *M. herus* had a greater richness of woody and forb species, but no difference in graminoid herbs (Poaceae and Cyperaceae) with the associated matrix. Contrasting findings were made for forb species richness in Zimbabwe on nests of *Macrotermes* spp. that had fewer forb species than the associated matrix of nutrient-poor granite soils. However, in the same study, no difference in forb species richness was detected in basalt soils (Muvengwi *et al.*, 2017). In the Worcester-Robertson valley, South Africa nests of *M. viator* were characteristically dominated by deciduous growth forms (succulent and non-succulent), and the matrix by succulent evergreen growth forms, while non-succulent evergreens were evenly distributed between the two habitats (Midgley and Musil, 1990).

The differences in plant species richness and dominant growth forms between termite nest and matrix habitats, and the presence of species that occur exclusively on termite nests affect landscape heterogeneity and diversity (Erpenbach *et al.*, 2013; Muvengwi *et al.*, 2017). Nests of *Macrotermes* sp. in miombo woodland, Zimbabwe have been identified as the initiator of various changes (physical and chemical soil properties) and subsequent spatial patterning of woody species, that increase local heterogeneity (Joseph *et al.*, 2013). The tree communities on nests of *M. subhyalinus* in Burkina Faso significantly improved landscape species density, diversity and community distribution (Traoré *et al.*, 2008; Traoré *et al.*, 2015). Following the work comparing the diversity of *Macrotermes* sp. nests with that of the surrounding matrix in Burkina Faso and Benin (Erpenbach *et al.*, 2013), where authors found that nests increasingly contributed to species diversity with increasing rainfall in Benin, community analyses were performed on nests and matrices of four different savanna types (*Crossopteryx*, *Detarium*, *Mitragyna* and *Terminalia* savannas) in Benin (Erpenbach *et al.*, 2017). Plant communities in matrices of all savanna types differed from that of *Macrotermes* sp. nests, the latter which also had several unique species not present in the matrices. The difference in plant communities between nest and matrix habitats, in all four savanna types, showed correlation with differences in soil parameters; pH, conductivity, and potassium concentration, while other soil parameters also correlated well for different savanna types (Erpenbach *et al.*, 2017).

### 5.1.2. The impact of termite nests on faunal communities

Vertebrates are attracted to termite nests for shelter (Pomeroy and Service, 1986; Moreira *et al.*, 2009; Simioni *et al.*, 2014) or greater resource availability for grazing (Smith and Yeaton, 1998; Holdo and McDowell, 2004; Seymour *et al.*, 2014). Physical changes to soil may also attract burrowing animals (Lovegrove and Siegfried, 1986; Lovegrove, 1991), and the presence of termites themselves attract a higher incidence of termitophagous animals (Louw *et al.*, 2017). Finally, termite nests offer higher ground, which offers protection from flooding in the matrix and improves visibility to facilitate anti-predator behaviours, making these preferred sites for middens of prey species e.g. blesbok (Coe and Carr, 1978). Nest soils of *Macrotermes michaelseni*, *Trinervitermes* sp. and *Microtermes* sp. in Hwange National Park, Zimbabwe have distinct plant communities with significantly higher foliar concentrations of Ca, Mg, K and P compared to the associated matrix, making these termite nests preferential feeding sites for elephants (Holdo and McDowell, 2004). These nests also harbour a significantly greater abundance and richness of smaller mammals, some of which were found exclusively on such nests (Fleming and Loveridge, 2003). However, little is known about how invertebrate communities respond either directly or indirectly to termite mounds. A review of the influence of termites in the Cerrado biome of Brazil on local herpetofauna found that 31 – 57 % of such species use termitaria either as permanent refugia, breeding sites, or feeding sites (Moreira *et al.*, 2009). The authors found a positive relationship between termite species richness and lizard species richness, however, they concluded that termite richness and abundance did not drive, but instead maintained, lizard richness (Colli *et al.*, 2006). Another study in the Miombo woodlands of Chizarira National Park, Zimbabwe found that although mean reptile species richness and abundance were not different between termitaria and the matrix (Heermans, 2010), certain species showed distinct habitat preferences e.g. *Ichnotropis* sp. and *Mabuya striata wahlbergii* on *Macrotermes* sp. mounds, and *Nucras holubi* in the matrix. Contrary to these findings, Fleming and Loveridge (2003) found that the abundance and species richness of both amphibians and reptiles in Miombo woodland was greater than that of associated *Macrotermes* nests, however, these differences were not significant.

The impact of termite nests on invertebrate communities has garnered more interest in recent years and show that invertebrate heterogeneity is positively correlated with subsequent chemical and physical changes in soil brought about by termite nests (Leitner *et al.*, 2020). Cornell (2014) found that invertebrate communities on *M. viator* nests were distinct from that of the surrounding matrix. This was attributed to a higher incidence of herbivorous invertebrates on nests, this in turn being a result of the associated higher plant productivity (Picker *et al.*, 2007). A study on ant communities in Zimbabwe found that the increased heterogeneity in plant communities caused by the presence of *Macrotermes* sp. nests facilitated the coexistence of distinct ant communities on nests compared to the associated matrix (Skidmore, 2010). A survey of orthopterans, beetles and ants associated with nests of *Macrotermes falciger* in Kruger National Park, South Africa found positive relationships between nest size and richness of associated orthopterans and beetles, with a greater abundance of beetles and ants on nests, and a significant difference between nest and matrix ant community compositions. Species richness of ants increased with increasing rainfall, while that of orthopterans decreased with increasing rainfall (Leitner *et al.*, 2020). In grasslands near Bloemfontein 82 species of spider where identified on nests of *T. trinveroides*. Spider abundance was found to correlate with differences in nest height, surface perforations of nests, and season, however, these findings were not compared with that of the associated matrix (Haddad and Dippenaar-Schoeman, 2002). More recently (Henschel and Lubin, 2018) determined that three species of web spider (*Isoxya cicatricose*, *Nemoscolus tubicola*, and *N. vigintipunctatus*) were more abundant on *M. viator* nests than the associated matrix in the Karoo. In addition, a significantly greater abundance of ants was collected from *M. viator* nests than the associated matrix at the same study site, however, the species richness showed no difference (Arena *et al.*, 2020).

### 5.1.3. Objectives

*M. viator* mounds are typically associated with distinct floral and faunal communities compared to their associated matrices (Midgley and Musil, 1990; Milton and Dean, 1990; Cornell, 2014; Arena *et al.*, 2020). This chapter describes and compares the plant and ant communities between *M. viator* mounds and their associated matrices from sites across a rainfall gradient. This chapter investigates how plant communities respond to soil modifications brought about by *M. viator* (Midgley and Musil, 1990), which were discussed in Chapter 3 and 4. For comparative purposes between sites with distinctly different plant species, similar analyses were performed using plant growth form data (Midgley and Van Der Heyden, 1999) to distinguish plant communities from nest and matrix habitats (Midgley and Musil, 1990; Milton, 1990). Using ants as an indicator taxon for invertebrates, the influence of *M. viator* mounds on invertebrate community composition, species richness and biomass are explored. The differences in plant and ant community composition along with species diversity and cover/abundance were expected to correlate with each other (Blatrix *et al.*, 2016; Cross *et al.*, 2016; Henschel and Lubin, 2018; Arena *et al.*, 2020).

## 5.2. Materials and methods

### 5.2.1. Study sites

The same sites previously used to measure the degree of soil enrichment and NDVI (Chapters 2 and 3) were used for plant and ant community data collection. These were Clanwilliam, Malmesbury, Koringberg, Tulbagh and Stellenbosch in the Fynbos biome, and Calitzdorp, Prince Albert, Vanrhynsdorp and Worcester in the Succulent Karoo biome, and a single site, Oudtshoorn, in the Albany Thicket Biome (Figure 5.1) (Mucina and Rutherford, 2006). Sites also represent a rainfall gradient (SAWS, 2018) as presented in Table 5.1.

**Table 5.1.** The mean annual precipitation (MAP) of each data collection site across a rainfall gradient between 2010 and 2018 (SAWS, 2018).

| Site | MAP (mm) |
|---|---|
| Prince Albert | 144,45 |
| Vanrhynsdorp | 162,88 |
| Clanwilliam | 182,20 |
| Calitzdorp | 244,73 |
| Oudtshoorn | 244,73 |
| Worcester | 285,79 |
| Malmesbury | 348,63 |
| Koringberg | 359,10 |
| Tulbagh | 777,65 |
| Stellenbosch | 1060,14 |

### 5.2.2. Plant and ant data collection

To describe the plant and ant communities on *M. viator* nest habitats and their associated matrices sampling was conducted from August – October 2018 using a line transect at 10 sites across a rainfall gradient (Table 5.1). The mean mound diameter for each *M. viator* nest investigated was determined from two measurements; diameter from north to south, and from east to west.

At each site a total of 20 transects were set out; 10 on separate *M. viator* mounds each paired with a transect in the associated matrix (at least 10 m away from nest boundaries). Each transect was 20 m in length, and where nests were too small for a single transect multiple lines (±1.5 m apart) were laid in parallel until a full 20 m was met. Using a 20 m tape measure along the length of each transect, the canopy cover of each plant species was

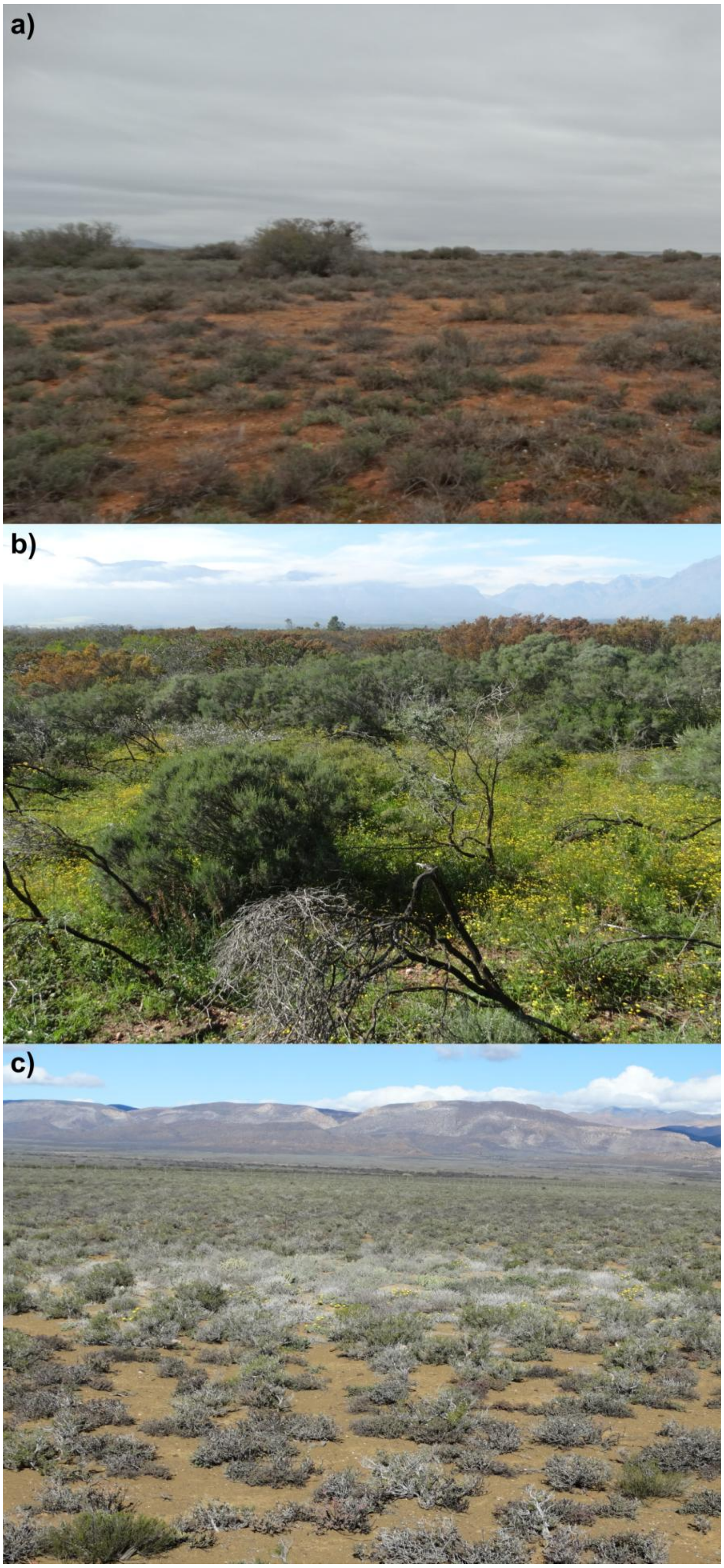

**Figure 5.1.** Heuweltjies in the **a)** Albany Thicket (Oudtshoorn), **b)** Fynbos (renosterveld in Tulbagh), and **c)** Succulent Karoo (Prince Albert) biomes.

recorded where it intersected the line, including overlapping plants. Some species were identified in the field, while others were identified later from photographs and field guides and recorded in Appendix M  (Vlok and Schutte-Vlok, 2015; Smith *et al.*, 2017; Manning, 2018).

To reduce the complexity of the data, plants were classified into growth forms (Appendix N) according to the classification described by Midgley and van der Heyden (1999). These groups are trees (phanerotypes), perennial grasses (hemicryptophytes), geophytes (cryptophytes), short-lived ephemeral herbs and annuals (therophytes),  and shrubs – which includes climbers, woody parasites, perennial shrubby graminoids, and perennial herbs (Midgley and Van Der Heyden, 1999). These groups were then further divided into subcategories of succulence (either non-succulent or as being leaf- or stem-succulent) and leaf retention (deciduous or evergreen).

### 5.2.3. Ant sampling

A total of 220 Falcon tubes (50 ml, 40 mm diameter) were filled (±15 ml) with a 50 % antifreeze solution (to preserve catch) to use as pitfall traps for small invertebrates, specifically ants. This method has been noted to yield a good representation of ant species richness (Samways, 1983; Arena *et al.*, 2020) and abundance (Rojas and Fragoso, 2000). The same *M. viator* nests and associated matrices used at each site to collect vegetation data were used to collected ant data (November 2017 – January 2018). Pitfall traps spaced 1 m apart, 10 on *M. viator* mounds and 10 in the associated matrix, were buried and left in the field for 72 h before being re-collected. The contents of traps were separated into ants and by-catch and stored at -20 °C in 70% ethanol. Ant species were initially separated into morpho-types and species then determined (Bolton, 1994; Slingsby, 2017).

### 5.2.4. Diversity pattern analyses

Using the collected plant and ant species and cover/abundance data, species accumulation and rarefaction curves (999 permutations) were produced (Appendix P) in R Statistical Software (version 3.6.1) using the ‘*vegan*’ package (Oksanen *et al.*, 2007) to assess the sampling effort. The sampling effort was further assessed by comparing the observed plant and ant species richness of each site with several richness estimates (Chao, first and second-order Jackknife, and Bootstrap) using Pearson’s product-moment correlation. These same data and software packages were then used to calculate plant and ant species diversity indices (Shannon-Wiener and Simpson) and evenness (Pielou).

The difference in mean richness, cover/abundance, and species diversity indices of plants and ants were tested by performing Type III (which tests the main effects, site and habitat, in the presence of interactions between- and within these effects) two-way Analyses of Variance (ANOVA) on the equal number of sites, and an equal number of paired habitat transects at each site. Post-hoc comparisons were made using Tukey's test to detect differences in these measures between sites and habitats. These analyses were performed and visualized in R Statistical Software (version 3.6.1) using the packages '*car*', '*devtools*' and '*ggpubr*' (Fox *et al.*, 2016; Wickham and Chang, 2016; Kassambara and Kassambara, 2019).

### 5.2.5. Community analyses

Plant and ant community structures were investigated using Plymouth Routines in Multivariate Ecological Research (PRIMER). The cover/abundance data of plant and ant species were log-transformed (log[x+1]). Using the SIMPER function in PRIMER two-way (site and habitat) crossed Bray-Curtis similarity percentages were calculated to give 1) the mean similarity between all transects (nest and matrix) at each site, 2) mean dissimilarity between all sites, and 3) mean similarity between nest and matrix transects across all sites. A one-way (habitat) Bray-Curtis similarity percentage was calculated for each site respectively to determine the 1) similarity between nest and matrix transects respectively, and 2) mean dissimilarity between nest and matrix transects for each site. The SIMPER analyses identified the dominant plant and ant species of each site, and each habitat (nest and matrix) for each site respectively. A Bray-Curtis similarity matrix was produced and, using the cluster function in PRIMER, used to generate dendrograms used to visualize ordinations. Plant and ant community distributions were visualized by producing a Non-metric Multi-Dimensional Scale (NMDS) ordinations (Clarke and Gorley, 2015). The strength (R) and the significance of the visualized groupings were tested using the Analysis of Similarity (ANOSIM) function in PRIMER.

## 5.3. Results

The mean sampling effort of plant species according to all species richness estimates (Chao, Jackknife 1 and 2, and Bootstrap) was 76 %, and that of ant species was 88 %. For both ant and plant datasets Jackknife 2 estimated species richness indicated the lowest sampling effort (84 and 69 % for ants and plants respectively), and Bootstrap estimated species richness the greatest sampling effort (92 and 88 % for ants and plants respectively). The respective estimated species richness values for both plants and ants were compared to observed species richness in Table 5.2. and the associated rarefaction curves presented in Appendix P.

**Table 5.2.** The observed species richness of plants and ants at each site compared to Chao, Jackknife of first and second-order, and Bootstrap estimated species richness and standard deviation (±) from 999 permutations.

| Plant species richness | | | | | |
|---|---|---|---|---|---|
| **Site** | **Observed** | **Chao** | **Jackknife1** | **Jackknife2** | **Bootstrap** |
| **Malmesbury** | 77 | 103,76 (±14,02) | 101,70 (±8,65) | 114,87 (N/A) | 88,29 (±4,72) |
| **Tulbagh** | 77 | 88,88 (±6,99) | 96,00 (±6,82) | 100,36 (N/A) | 86,49 (±4,35) |
| **Clanwilliam** | 73 | 118,87 (±25,89) | 97,70 (±6,52) | 115,13 (N/A) | 83,58 (±3,13) |
| **Vanrhynsdorp** | 73 | 95,84 (±12,10) | 96,75 (±7,53) | 108,17 (N/A) | 83,87 (±3,68) |
| **Stellenbosch** | 59 | 88,69 (±16,09) | 82,75 (±8,37) | 96,72 (N/A) | 69,35 (±4,27) |
| **Koringberg** | 55 | 83,74 (±16,80) | 75,90 (±6,23) | 88,88 (N/A) | 64,14 (±3,10) |
| **Worcester** | 52 | 71,24 (±12,16) | 69,10 (±5,44) | 78,48 (N/A) | 59,76 (±2,90) |
| **Calitzdorp** | 33 | 50,10 (±13,70) | 44,40 (±4,72) | 51,79 (N/A) | 37,98 (±2,51) |
| **Oudtshoorn** | 28 | 29,71 (±1,99) | 33,70 (±2,70) | 30,57 (N/A) | 31,47 (±1,93) |
| **Prince Albert** | 28 | 54,60 (±20,39) | 35,60 (±3,32) | 42,80 (N/A) | 31,06 (±1,68) |
| **Ant species richness** | | | | | |
| **Koringberg** | 23 | 26,80 (±5,05) | 26,80 (±2,35) | 28,70 (N/A) | 24,90 (±1,44) |
| **Prince Albert** | 20 | 22,14 (±3,24) | 22,85 (±1,65) | 23,85 (N/A) | 24,46 (±1,21) |
| **Clanwilliam** | 17 | 17,95 (±2,19) | 18,90 (±1,34) | 20,70 (N/A) | 17,72 (±0,67) |
| **Stellenbosch** | 17 | 22,70 (±6,18) | 22,70 (±3,33) | 25,54 (N/A) | 19,53 (±1,65) |
| **Vanrhynsdorp** | 17 | 19,14 (±3,24) | 19,85 (±1,65) | 20,85 (N/A) | 18,40 (±1,03) |
| **Calitzdorp** | 16 | 18,14 (±3,24) | 18,85 (±1,65) | 19,85 (N/A) | 17,40 (±0,98) |
| **Malmesbury** | 16 | 16,95 (±1,79) | 17,90 (±1,93) | 18,00 (N/A) | 16,97 (±1,08) |
| **Worcester** | 16 | 18,85 (±4,34) | 18,85 (±1,65) | 21,55 (N/A) | 17,13 (±0,86) |
| **Tulbagh** | 14 | 14,16 (±0,52) | 14,95 (±0,95) | 13,29 (N/A) | 14,82 (±0,84) |
| **Oudtshoorn** | 13 | 13,95 (±2,18) | 14,90 (±1,34) | 16,70 (N/A) | 13,77 (±0,74) |

### 5.3.1. Vegetation line transects

#### 5.3.1.1. Species richness

A total of 376 plant species were identified from 10 matrix and 10 *M. viator* nest transects across all 10 sites (Appendix M). The highest number of plant species (77) was found in Malmesbury and Tulbagh, and the lowest number of plant species (28) in Oudtshoorn and Prince Albert. The mean number of plant species per transect line is shown in (Figure 5.2). The two-way ANOVA found a significant interaction between site and habitat, and Tukey

HSD posthoc test determined that only the difference in mean species richness in Calitzdorp was significant ($p < 0.001$). In Calitzdorp matrix transects had a higher (10) mean number of species per transect compared to mound transects (3).

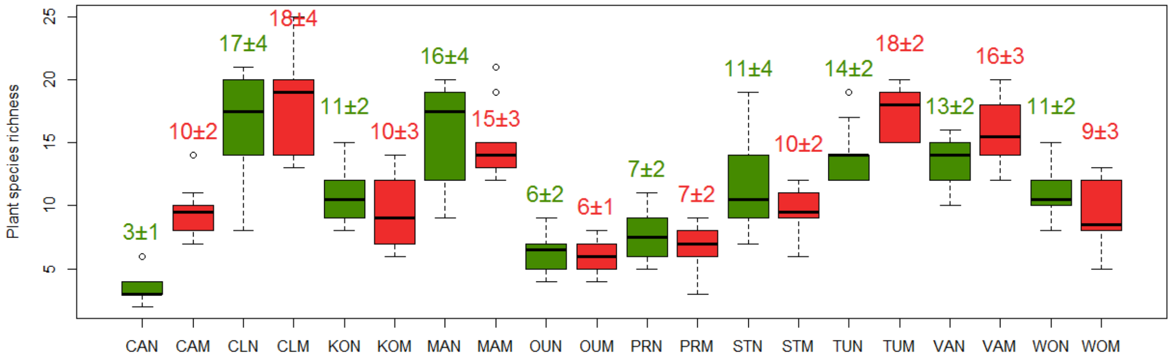

**Figure 5.2.** Mean and standard deviation (±) of plant species richness of *M. viator* mounds (green) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO) followed by either an 'N' for mound (nest) or 'M' for matrix habitats.

Unique species that occur exclusively in one habitat of their respective sites were found at all sites. The greatest overall contrast was found in Tulbagh, where matrix habitats harboured 42 plant species not encountered in mound habitats, and mound habitats had 21 species not encountered in matrix habitats. Tukey's HSD posthoc test found this difference in the number of unique species between habitats in Tulbagh to be significant ($p < 0.05$), and also Calitzdorp ($p < 0.001$) where matrix habitats had 20 species, and mounds 7 species found only in these respective habitats at the site. The mean number of unique species encountered per transect are presented in Figure 5.3.

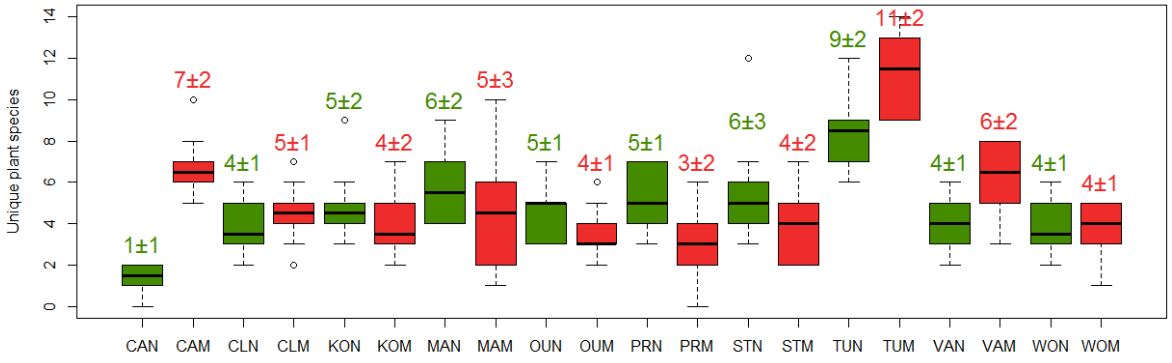

**Figure 5.3.** The mean and standard deviation (±), number of species unique to *M. viator* mounds (green) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO) followed by either an 'N' for mound (nest) or 'M' for matrix habitats.

### 5.3.1.2. Plant cover

In total mound, habitats had a greater plant cover (2.3 km), compared to matrix habitats (1.9 km). The site with the most cover was Tulbagh (661 m), and the site with the lowest plant cover was Calitzdorp (195 m), the latter of which was highly over-grazed by ostriches. Tukey's HSD posthoc test identified three sites where the difference in cover was significant ($p$ < 0.001). In Calitzdorp matrix habitats had significantly greater plant cover than mound habitats, while the opposite was true in Koringberg and Tulbagh, here mound habitats had significantly greater plant cover than the associated matrix habitats (Figure 5.4).

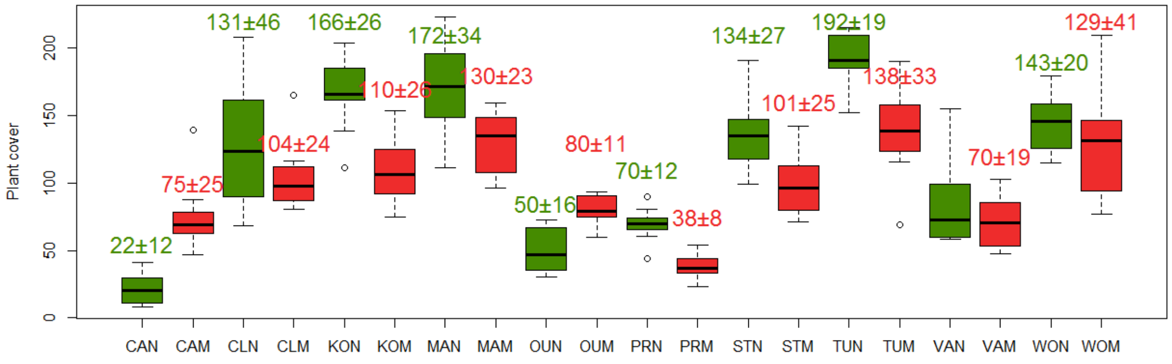

**Figure 5.4.** The mean and standard deviation (±) of plant cover on *M. viator* mounds (green) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO) followed by either an 'N' for mound (nest) or 'M' for matrix habitats.

### 5.3.1.3. Plant diversity

The highest total mean Shannon diversity was found in Clanwilliam (2.020 ±0.277, MAP = 182 mm) compared to a mean Simpson diversity of 0.797 (±0.059), and the highest mean Simpson diversity was found in Tulbagh (0.804 ±0.047, MAP = 778 mm) compared to a mean Shannon diversity of 2.005 (±0.229). Calitzdorp, with a MAP of 245 mm, had the lowest Shannon and Simpson diversity scores of 1.358 (±0.537) and 0.654 (±0.176) respectively. The mean diversity of transects in each habitat and at each site are presented in Figure 5.5. Both the mean Shannon Weiner and Simpson's diversity indices were significantly (*p* < 0.001, Tukey's HSD) greater in matrix habitats of Calitzdorp compared to mound habitats, while no other significant differences were found.

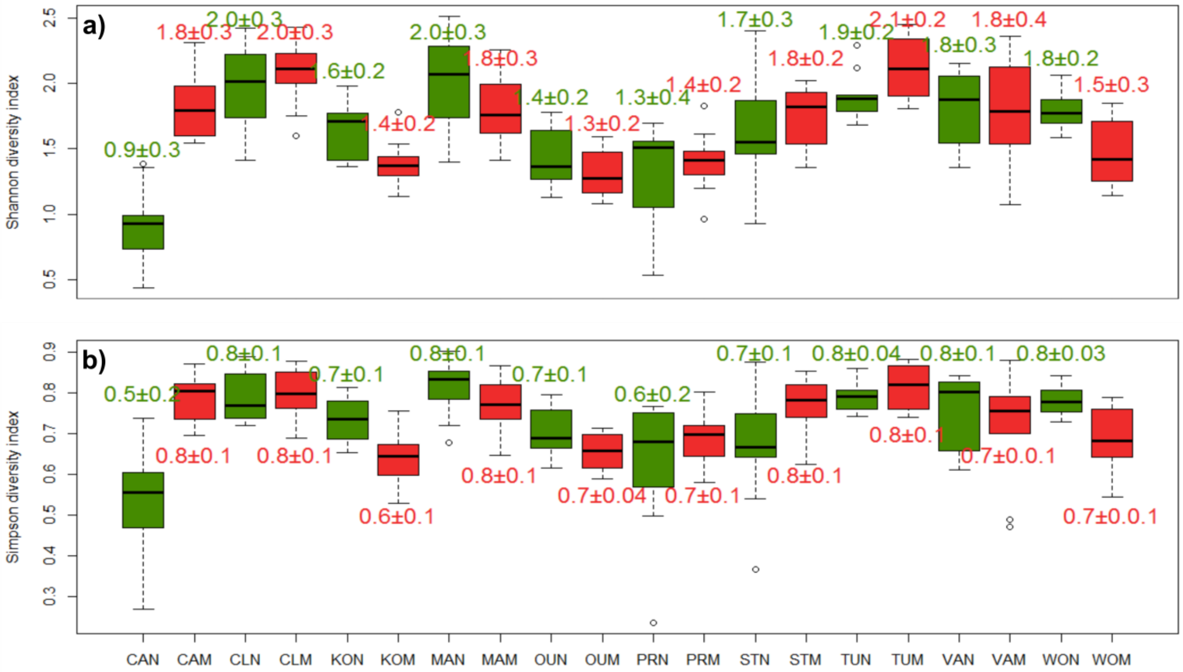

**Figure 5.5.** The mean and standard deviation (±) **a)** Shannon and **b)** Simpson diversity indices of *M. viator* mounds (green) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO) followed by either an 'N' for mound (nest) or 'M' for matrix habitats.

### 5.3.1.4. Plant community analysis

The respective matrix plant communities from 10 sites had a mean SIMPER similarity of 49.5 (±7.5) %, and mound communities had a mean similarity of 47.7 (±9.4) %. The mean dissimilarity between plant communities of matrix and mound was 79.6 (±6.4) %. All sites were visualized using Non-Metric Multi-Dimensional Scaling ordinations as represented by that of sites used in this study with the highest (Stellenbosch) and lowest (Prince Albert) mean annual precipitation, from the Succulent Karoo and Fynbos, respectively (Figure 5.6).

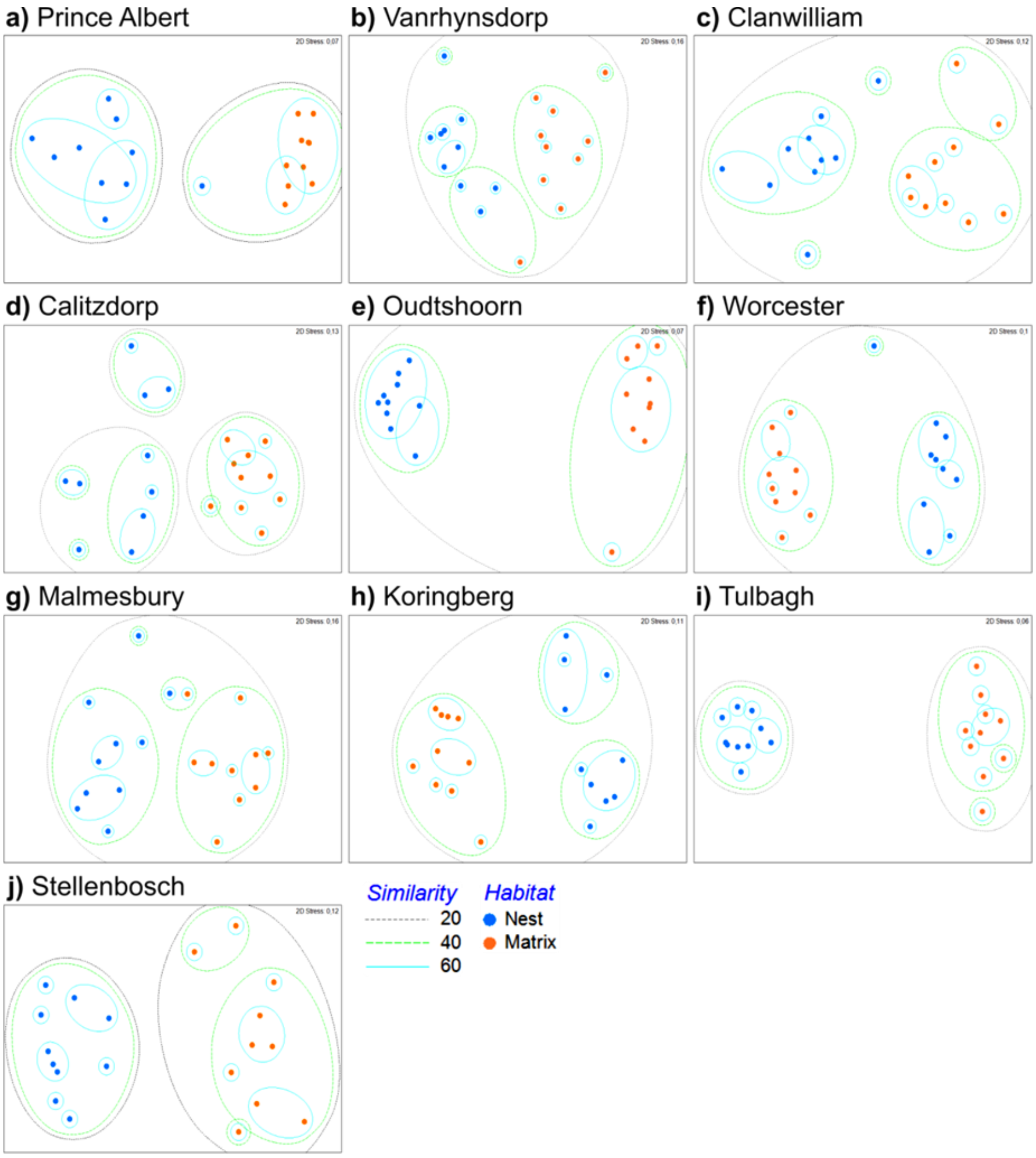

**Figure 5.6.** Non-Metric Multi-Dimensional Scaling ordinations of plant communities on *M. viator* mounds (blue) and their associated matrices (orange) along a rainfall gradient from low to high (a – j). Clustering shown at 20 % (black line), 40 % (green line) and 60 % (blue line) SIMPER similarity.

Matrix communities across sites showed only 11.7 % global similarity (across all sites), and mound communities only 10.3 %. However, the global dissimilarity between mound and matrix communities was 87.7 % following SIMPER analysis. The five plant species that contributed most to among-sample-similarity at the respective sites are shown in Table 5.3.

**Table 5.3.** List of top five plant species (and dead plant tissues that could not be identified) that contributed to the respective similarity of each of the ten sites and their respective habitats according to Bray-Curtis similarity.

| | Site | Nest | Matrix |
|---|---|---|---|
| **Calitzdorp** | Dead | Dead | *Leipoldtia schultzei* |
| | *Cynanchum viminale* | *Malephora lutea* | *Cynanchum viminale* |
| | *Lycium ferocissimum* | *Pteronia pallens* | *Lycium ferocissimum* |
| | *Malephora lutea* | *Cynanchum viminale* | *Pentzia incana* |
| | *Leipoldtia schultzei* | - | *Ruschia spinosa* |
| **Clanwilliam** | *Adenogramma glomerata* | *Searsia incise* | *Elytropappus rhinocerotis* |
| | *Elytropappaus rhinocerotis* | *Diascia longicornis* | *Ehrharta villosa* |
| | *Heliophila variabilis* | *Moraea minuata* | *Tetraria* sp. |
| | *Oxalis depressa* | *Adenogramma glomerata* | *Ursinia anthemoides* |
| | *Tetragonia rosea* | *Dimorphotheca sinuate* | *Aspalathus spinosa* |
| **Koringberg** | *Oxalis pes-caprae* | *Bromus hordaceus* | *Cenchrus* sp. |
| | *Cenchrus* sp. | *Oxalis pes-caprae* | *Elytropappus rhinocerotis* |
| | *Elytropappaus rhinocerotis* | *Trachyandra muricata* | *Eriocephalus africanus* |
| | *Eriocephalus africanus* | *Chlorophytum triflorum* | Dead |
| | *Bromus hordaceus* | *Eriocephalus rhinocerotis* | *Ruschia pungens* |
| **Malmesbury** | *Ehrharta calycina* | *Oxalis pes-caprae* | *Eriocephalus africanus* |
| | *Eriocephalus africanus* | *Ehrharta longiflora* | *Ehrharta calycina* |
| | *Elytropappaus rhinocerotis* | *Ehrharta calycina* | *Elytropappus rhinocerotis* |
| | *Oxalis pes-caprae* | *Elytropappus rhinocerotis* | *Restio capensis* |
| | *Ehrharta longiflora* | *Helichrysum cymosum* | *Ehrharta longiflora* |
| **Oudtshoorn** | Dead | *Tetraena chrysopteros* | *Ruschia pungens* |
| | *Ruschia pungens* | *Aizoon* sp. | Dead |
| | *Tetraena chrysopteros* | Dead | *Leipoldtia schultzei* |
| | *Aizoon* sp. | *Mesembryanthemum junceum* | *Cynanchum viminale* |
| | *Leipoldtia schultzei* | *Malephora lutea* | - |
| **Prince Albert** | *Pteronia pallens* | *Malephora lutea* | *Osteospermum sinutaum* |
| | *Ruschia spinosa* | *Mesembryanthemum crystallinum* | *Ruschia spinosa* |
| | *Osteospermum sinuatum* | *Lampranthus uniflorus* | *Pteronia pallens* |
| | *Malephora lutea* | *Galium capense* | *Crassula subaphylla* |
| | *Mesembryanthemum crystallinum* | *Ruschia spinosa* | *Galenia papulosa* |
| **Stellenbosch** | *Cliffortia atrata* | *Searsia angustifolia* | *Erica imbricata* |
| | *Searsia angustifolia* | *Cliffortia atrata* | *Muraltia heisteria* |
| | *Ehrharta calycina* | *Ehrharta calycina* | *Seriphium plumosum* |
| | *Seriphium plumosum* | Dead | *Elytropappus rhinocerotis* |
| | *Erica imbricata* | *Hordeum murinum* | *Restio capensis* |
| **Tulbagh** | *Oxalis pes-caprae* | *Oxalis pes-caprae* | *Erica cerinthoides* |
| | *Anthospermum aethiopicum* | *Ehrharta calycina* | *Leucadendron rubrum* |
| | *Ehrharta calycina* | *Senecio erosus* | *Anthospermum aethiopicum* |
| | *Eriocephalus africanus* | *Hermannia scabra* | *Muraltia heisteria* |
| | *Erica cerinthoides* | *Aizoon africanum* | *Oxalis obtusa* |
| **Vanrhynsdorp** | *Hoplophyllum spinosum* | *Stipa capensis* | *Aizoon africanum* |
| | *Ursinia nana* | *Hoplophyllum spinosum* | *Gorteria diffusa* |
| | *Gorteria diffusa* | *Ursinia nana* | *Hoplophyllum spinosum* |
| | *Stipa capensis* | *Malephora pupureo-crocea* | *Ursinia anthemoides* |
| | *Tetragonia fruticosa* | *Cotula turbinate* | *Enneapogon scaber* |
| **Worcester** | *Dead* | Dead | *Pteronia pallens* |
| | *Euphorbia mauritanica* | *Ehrharta calycina* | Dead |
| | *Pteronia pallens* | *Tylecodon paniculata* | *Euphorbia mauritanica* |
| | *Ehrharta calycina* | *Pteronia incana* | *Aristida* sp. |
| | *Aristida* sp. | *Aloe microstigma* | *Ruschia caroli* |

### 5.3.2. Ants collected from pitfall traps

#### 5.3.2.1. Species richness and abundance

A total of 62 species of ants were identified from a total of 67 965 ants collected from 10 matrix and 10 *Microhodotermes viator* nest transects across 10 sites (Appendix O). Koringberg had the greatest ant species richness of 22 species, and Oudtshoorn the lowest with only 12 species. The mean species richness of transects is shown in Figure 5.7., however, no significant difference was detected between habitats at their respective sites ($p$ > 0.05, Tukey's HSD).

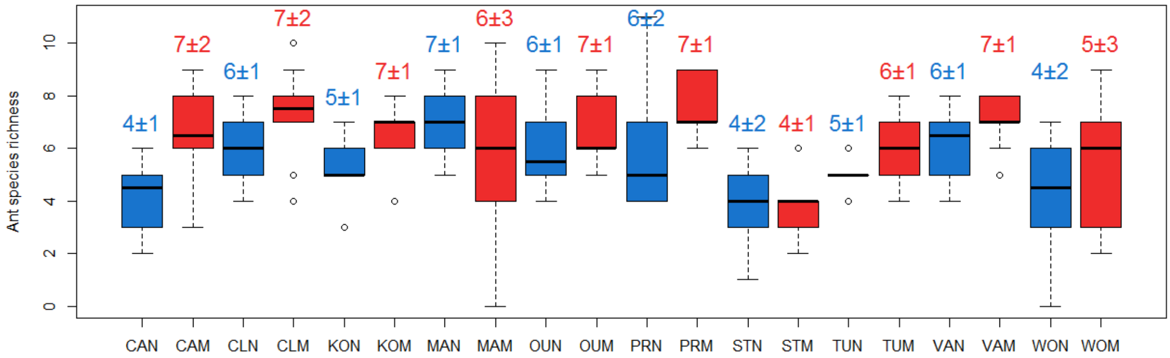

**Figure 5.7.** Mean and standard deviation (±) of ant species richness of *M. viator* mounds (blue) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO).

Aside from the mound habitats of Malmesbury and Tulbagh, every other habitat had unique ant species not encountered in the other habitat at their respective sites. The biggest contrast was found in Calitzdorp where matrix habitats had six species not encountered in mound habitats, and the latter had one species not found in matrix habitats. The mean number of such unique species encountered in transects is shown in Figure 5.8., however, none of these was significantly different between habitats ($p$ > 0.05, Tukey's HSD).

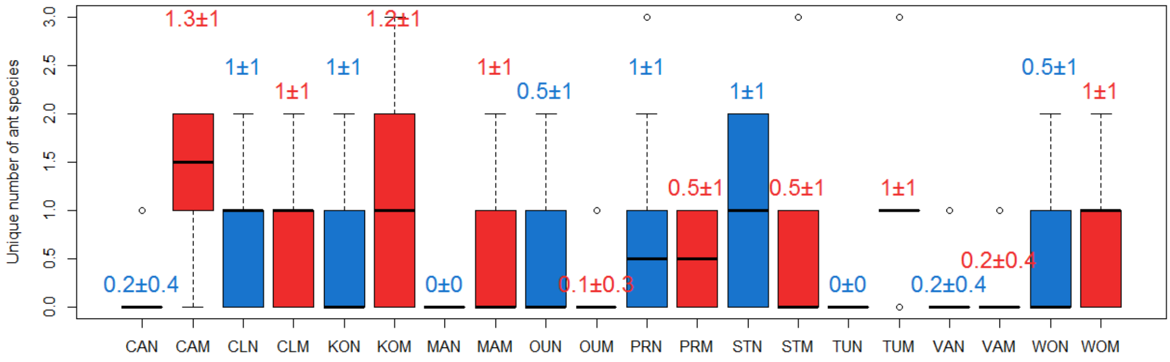

**Figure 5.8.** The mean and standard deviation (±), for the number of ant species unique to *M. viator* mounds (blue) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO).

### 5.3.2.2. Ant abundance

In total matrix habitats yielded the greatest abundance of ants (37022) compared to mound habitats (30943), and the site where most ants were captured (20722) was Koringberg, and the least in Prince Albert (977). The mean number of ants caught per transect is shown in Figure 5.9., however, Tukey's HSD posthoc test found no significant difference in means between habitats (*p* > 0.05).

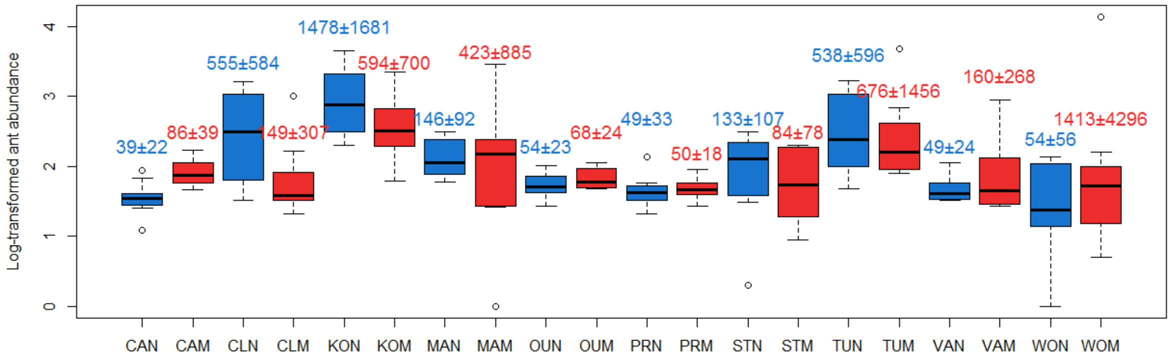

**Figure 5.9.** The mean and standard deviation (±) of plant cover on *M. viator* mounds (blue) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO).

### 5.3.2.3. Ant species diversity

The highest mean Shannon Weiner diversity (1.3562 ±0.4376) of ants were found in Vanrhynsdorp, which had a Simpson's diversity of 0.6419 (±0.2058). The highest Simpson's diversity was found in Oudtshoorn (0.6677 ±0.7510), which had a Shannon Weiner diversity value of 1.3464 (±0.1736). The mean ant Shannon Weiner and Simpson diversity indices of mound and matrix habitats at each site are presented in Figure 5.10., however, none of the differences in diversity indices between habitats was significant (*p* > 0.05, Tukey's HSD).

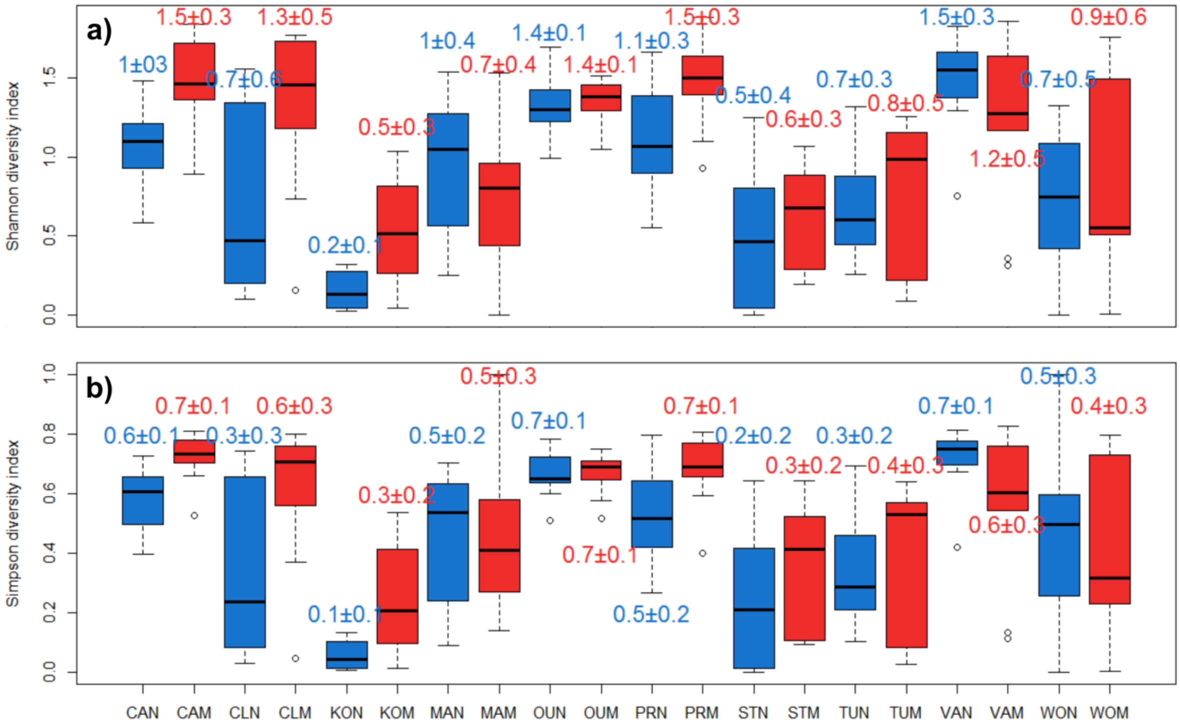

**Figure 5.10.** The mean and standard deviation (±) **a)** Shannon and **b)** Simpson diversity indices of *M. viator* mounds (blue) and their associated matrices (red) at their respective sites; Calitzdorp (CA), Clanwilliam (CL), Koringberg (KO), Malmesbury (MA), Oudtshoorn (OU), Prince Albert (PR), Stellenbosch (ST), Tulbagh (TU), Vanrhynsdorp (VA), and Worcester (WO).

### 5.3.2.4. Ant community composition

The mean SIMPER similarity in ant community composition between mound habitats (55.6 %) was similar to that of matrix habitats (53.3 %), and the dissimilarity between mound and matrix habitats was less marked in ant communities (48.9 %) compared to plant communities. Clustering of ant communities as seen in NMDS-ordinations was also less marked than that of plant communities, and are either random as in Prince Albert, or hyperclustered as in Stellenbosch (Figure 5.11). The latter is probably the result of pitfall traps being randomly placed near ant nests, causing a skewed distribution.

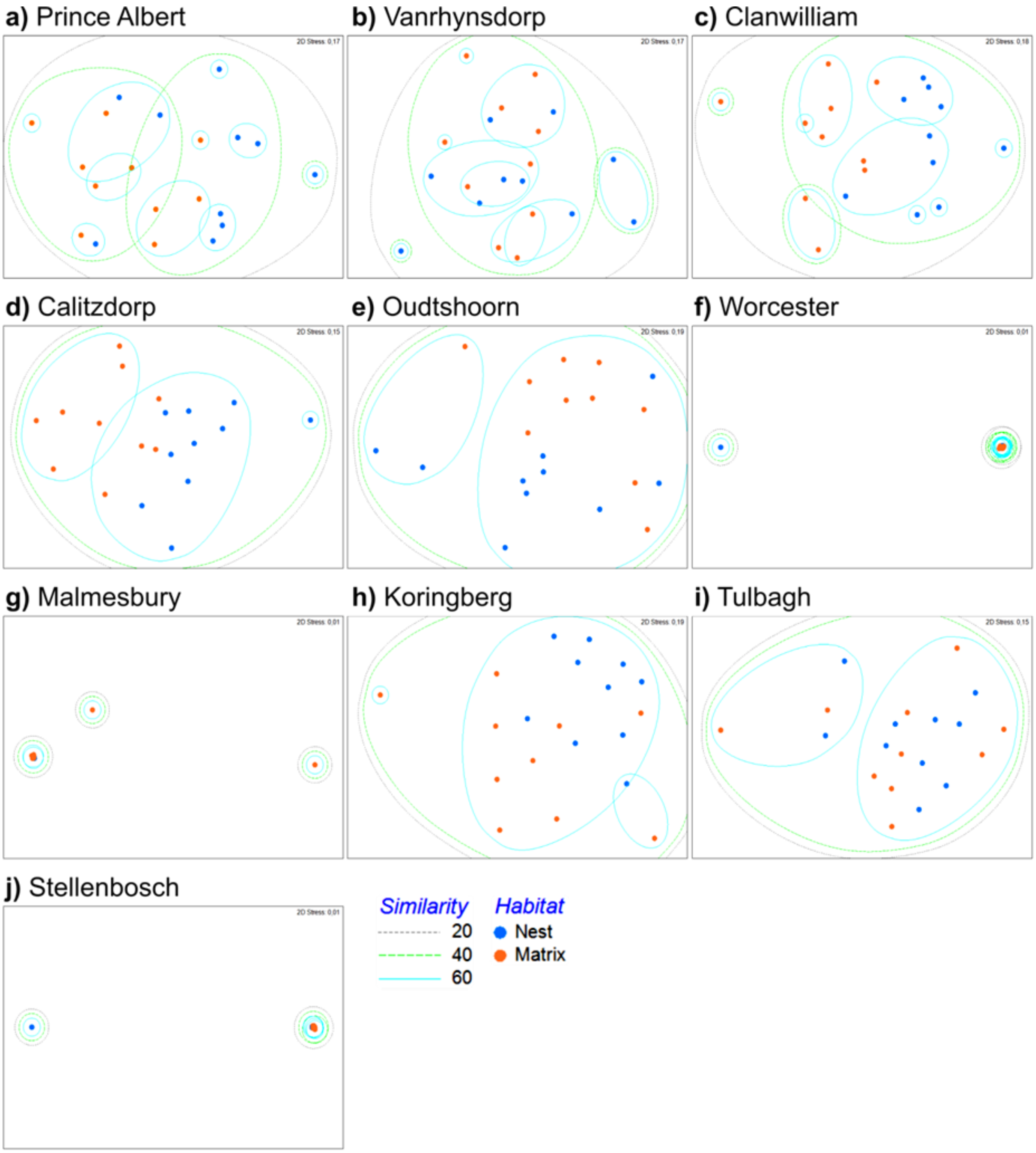

**Figure 5.6.** Non-Metric Multi-Dimensional Scaling ordinations of ant communities on *M. viator* mounds (blue) and their associated matrices (orange) along a rainfall gradient from low to high (a – j). Clustering shown at 20 % (black line), 40 % (green line) and 60 % (blue line) SIMPER similarity.

Matrix communities showed a global SIMPER similarity of 22.4%, and mound communities 23.0 %, compared to 77.5 % global dissimilarity between mound and matrix ant communities composition. SIMPER analysis identified the ant species that contributed most to the among-sample similarity at respective sites (Table 5.4).

### 5.3.3. Plant growth forms

Non-succulent evergreen shrubs, which was the dominant growth form, had significantly ($p < 0.05$, Mann-Whitney U) greater cover in matrix habitats (960 ±802 cm) than mound habitats (799 ±685 cm). This was the only growth form with significantly greater cover in matrix habitats. Both stem succulent (87 ±169 cm) and deciduous leaf succulent shrubs (52 ±131 cm) had significantly ($p < 0.05$, Mann-Whitney U) greater cover on mound habitats compared to matrix habitats (25 ±73 cm and 17 ±50 cm, respectively). Both deciduous leaf succulent (39 ±81 cm) and non-succulent therophytes (347 ±509 cm) also had significantly ($p < 0.001$, Mann-Whitney U) greater cover in mound than matrix habitats (3 ±12 cm and 108 ±252 cm, respectively). Finally, geophytes also had significantly ($p < 0.001$, Mann-Whitney U) greater cover in mound (372 ±596 cm) than matrix habitats (76 ±153 cm). Despite these stark differences in most growth forms mound habitats had 49.3 % global SIMPER similarity, and matrix habitats had 54.8 % global similarity, and the dissimilarity between these two habitats was 49.4 %.

**Table 5.4.** List of top five (where available) ant species that contributed to the respective similarity of each of the ten sites and their respective habitats according to Bray-Curtis similarity.

| | Site | Nest | Matrix |
|---|---|---|---|
| **Calitzdorp** | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| | *Linepithema humile* | *Linepithema humile* | *Monomorium australe* |
| | *Monomorium australe* | *Monomorium australe* | *Linepithema humile* |
| | *Pheidole tenuinodis* | - | *Pheidole tenuinodis* |
| | - | - | *Anoplolepis rufescens* |
| **Clanwilliam** | *Crematogaster melanogaster* | *Crematogaster melanogaster* | *Crematogaster melanogaster* |
| | *Tetramorium rufescens* | *Tetramorium rufescens* | *Ocymyrmex barbiger* |
| | *Ocymyrmex barbiger* | *Monomorium macrops* | *Tetramorium rufescens* |
| | *Pheidole tenuinodis* | *Monomorium xanthognathum* | *Pheidole tenuinodis* |
| | *Monomorium macrops* | *Monomorium australe* | *Mesoponera caffraria* |
| **Koringberg** | *Monomorium australe* | *Monomorium australe* | *Monomorium australe* |
| | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| | *Pheidole capensis* | - | *Pheidole capensis* |
| | - | - | *Camponotus mystaceus* |
| **Malmesbury** | *Pheidole capensis* | *Pheidole capensis* | *Pheidole capensis* |
| | *Tetramorium solidinum* | *Tetramorium solidinum* | *Tetramorium solidinum* |
| | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Anoplolepis custodiens* |
| | *Monomorium macrops* | *Monomorium macrops* | *Lepisiota capensis* |
| | *Lepisiota capensis* | *Lepisiota capensis* | *Ocymyrmex barbiger* |
| **Oudtshoorn** | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| | *Monomorium australe* | *Monomorium australe* | *Monomorium australe* |
| | *Camponotus fulvipilosus* | *Camponotus fulvipilosus* | *Anoplolepis rufescens* |
| | *Tetramorium signatum* | *Tetramorium signatum* | *Camponotus fulvipilosus* |
| | *Anoplolepis rufescens* | - | *Pheidole tenuinodis* |
| **Prince Albert** | *Ocymyrmex barbiger* | *Tetramorium signatum* | *Crematogaster schultzei* |
| | *Tetramorium signatum* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| | *Crematogaster schultzei* | *Pheidole tenuinodis* | *Lepisiota capensis* |
| | *Pheidole tenuinodis* | *Monomorium australe* | *Tetramorium signatum* |
| | *Lepisiota capensis* | *Monomorium delagoense* | *Monomorium australe* |
| **Stellenbosch** | *Pheidole capensis* | *Pheidole capensis* | *Pheidole capensis* |
| | *Lepisiota capensis* | *Lepisiota capensis* | *Lepisiota capensis* |
| | *Tetramorium solidinum* | *Tetramorium sericeiventre* | *Tetramorium solidinum* |
| **Tulbagh** | *Pheidole capensis* | *Pheidole capensis* | *Pheidole capensis* |
| | *Tetramorium solidinum* | *Tetramorium solidinum* | *Tetramorium solidinum* |
| | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| | *Camponotus fulvipilosus* | *Camponotus fulvipilosus* | *Technomyrmex pallipes* |
| **Vanrhynsdorp** | *Tetramorium rufescens* | *Crematogaster melanogaster* | *Tetramorium rufescens* |
| | *Ophthalmopone hottentota* | *Monomorium esharre* | *Ophthalmopone hottentota* |
| | *Crematogaster melanogaster* | *Ophthalmopone hottentota* | *Crematogaster melanogaster* |
| | *Monomorium esharre* | *Tetramorium rufescens* | *Pheidole tenuinodis* |
| | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| **Worcester** | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* | *Ocymyrmex barbiger* |
| | *Anoplolepis custodiens* | *Anoplolepis custodiens* | *Anoplolepis custodiens* |
| | *Meranoplus peringueyi* | *Monomorium australe* | *Meranoplus peringueyi* |
| | *Monomorium australe* | *Meranoplus peringueyi* | *Tetramorium erectum* |
| | *Ocymyrmex barbiger* | - | *Monomorium australe* |

### 5.3.4. Plant and ant community regressions

There was no significant relationship between plant species richness and either rainfall, spring- or autumn productivity. Plant cover, however, had significantly positive relationships with rainfall (cor = 38.67, $p < 0.001$) and both spring (cor = 36.13, $p < 0.001$) and autumn productivity (cor = 23.24, $p < 0.001$). Plant diversity (Shannon Weiner) also showed significant (cor = 17.58, $p < 0.05$) correlation with rainfall (Figure 5.12).

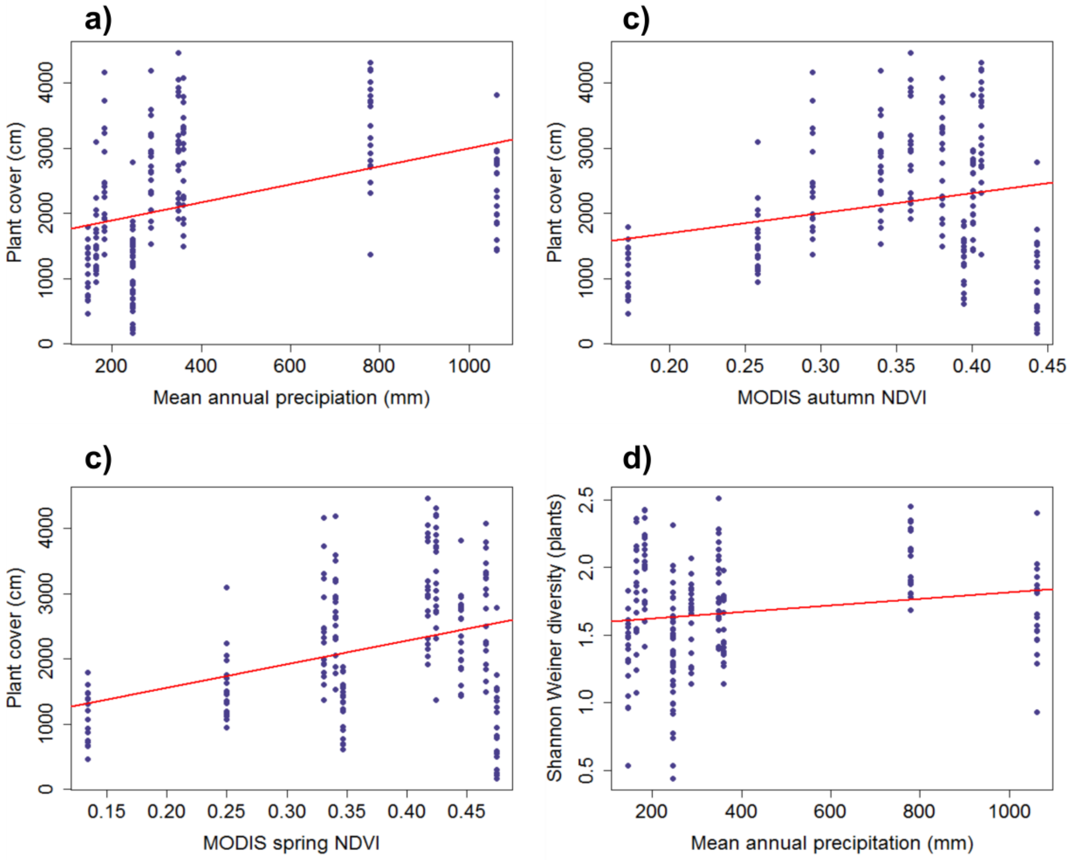

**Figure 5.7.** Pearson product-moment correlation regression showing the relationship of plant cover (cm) with a) Rainfall, **b)** Autumn productivity, and **c)** Spring productivity, and between **d)** Shannon Weiner plant diversity and rainfall.

None of the ant community variables showed any correlation with environmental variables. However, ant abundance had a significantly positive relationship with plant cover (cor = 13.95, $p < 0.05$), and species richness of ants also had a significant positive relationship (cor = 15.00, $p < 0.05$) with plant species richness (Figure 5.13).

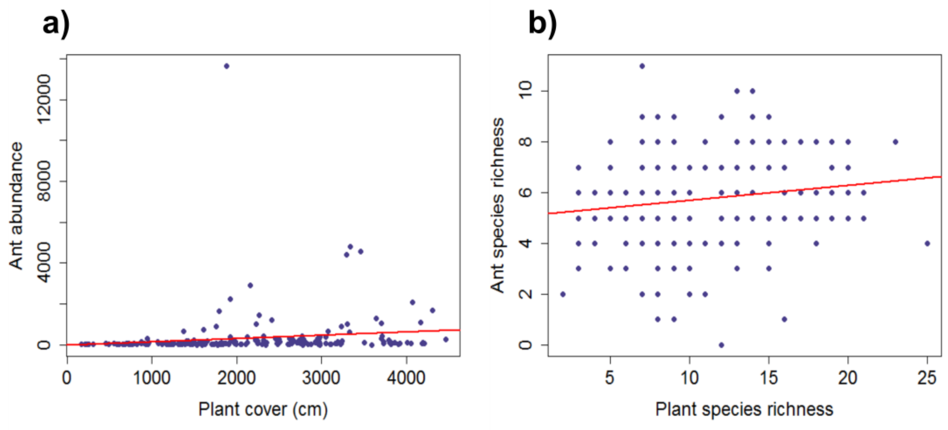

**Figure 5.13.** The relationship between a) Ant abundance and plant cover, and b) Ant and plant species richness.

## 5.4. Discussion

### 5.4.1. Do *M. viator* mounds promote plant diversity and productivity?

The total species richness of plant species for *M. viator* nest habitats in three sites (Koringberg, Stellenbosch and Worcester) was greater than that of their associated matrices, However, for all of the other sites, there was little difference in species richness between habitats. In Calitzdorp however, mounds had less species richness than the associated matrix, however, this was attributed to disturbance in the form of over-grazing by ostrich (Milton *et al.*, 1994). Despite only finding few cases of different plant richness and cover on mounds compared to matrices, NMDS ordinations support the hypothesis that these associated plant communities are distinctly different (Midgley and Musil, 1990; Milton and Dean, 1990). Differences are accounted for in terms of the presence/absence of species unique to each habitat and/or the importance value based on the cover. Differences in plant species cover have been attributed to adaptive differences in growth forms to local disturbance (Sobrado, 1991; Turner, 2003; Schmiedel *et al.*, 2016).

Consistent with previous findings (Fox *et al.*, 2005) there was a positive relationship between plant cover and rainfall, however, very little of the variation in plant cover is explained by rainfall. This could be due to additional mechanisms influencing these relationships in the different vegetation types (Esler *et al.*, 2015). In the Fynbos biome, communities are influenced by fire, which provides nutrients in an otherwise nutrient-poor environment despite moderate to high rainfall (Richards *et al.*, 1997; Mucina and Rutherford, 2006). In the Succulent Karoo biome, plant communities are primarily driven by water, which is necessary to moderate nutrient uptake (Bobbink *et al.*, 2010; Seymour *et al.*, 2019). Plant communities in the lowlands of the Albany Thicket biome are influenced primarily by frost (Duker *et al.*, 2015). These biome level influences govern plant responses to rainfall, and at the site and even transect level, there are more variables that further explain the residuals of an otherwise positive relationship between plant cover and rainfall, including local variation in physical and chemical properties of soil (Midgley and Musil, 1990; Dangerfield *et al.*, 1998; Bekker *et al.*, 2016). Plant cover of both matrix and mound habitats correlated significantly with both spring and autumn productivity.

Considering the costs of producing and maintaining leaves for deciduous plants (Sobrado, 1991) it was interesting to find that the only evergreen growth form to show significant association with a particular habitat would occur in matrix habitats, while deciduous plants dominated on enriched *M. viator* mounds (Midgley and Musil, 1990; Bekker *et al.*, 2016). This demonstrates another variable in the complex mechanism of selective pressure that drives distinct communities on mounds and ultimately promote diversity.

### 5.4.2. The influence of *M. viator* mounds on invertebrate communities

Ant community composition was not as different between the two habitats as was plant community composition. Although no differences in species richness, diversity or abundance of ants were confirmed, SIMPER analysis determined there is a considerable dissimilarity between the mound and matrix ant communities and a positive relationship between total ant abundance and total plant cover was found. Arena *et al*. (2020) were able to demonstrate a greater abundance of ants *M. viator* mounds in Prince Albert, one of the study sites investigated in this study as well. Changes in abundance have been the dominant response to termite mounds in invertebrate communities, especially ants (Leitner *et al.*, 2020). It is possible abundance effects were masked by a seasonal fluctuation of activity as is known to occur in the Karoo (Steinberger *et al.*, 1992; Lindsey and Skinner, 2001). It is unlikely however that such a fluctuation would occur simultaneously across all sites. Compared to the study in Prince Albert, which had 500+ trapping days compared to three in this study for all sites, it is possible longer trapping periods would have yielded more marked effects in ant communities across mound and matrix habitats. In the Fynbos *A. custodiens*, *P. capensis* and *L. humile* have been identified as dominant species (Donnelly, 1985). The former two species were also dominant in two (Malmesbury and Tulbagh) of the six (Clanwilliam, Koringberg, Stellenbosch and parts of Vanrhynsdorp) sites in the Fynbos biome (Mucina and Rutherford, 2006) while *L. humile* was dominant in Calitzdorp. Neither of these species was present at Clanwilliam or Vanrhynsdorp, while *P. capensis* was present at Koringberg it was also a dominant species in Stellenbosch which also had *L. humile* present.

## 5.5. Conclusion

Mounds of *M. viator* are inherently associated with various physical and chemical modifications, and thus introduce heterogeneity to the landscape (Midgley and Musil, 1990; McAuliffe *et al.*, 2019). Given the presence of unique plant and ant species on these mounds, which are engineered structures, these mounds introduce additional heterogeneity which could potentially increase species diversity (Erpenbach *et al.*, 2013; Joseph *et al.*, 2014). The fact that deciduous plants, that can efficiently exploit soil conditions of these enriched soil, dominated mounds in this study, demonstrates one example of a process that could increase species diversity and alter community structure. These properties make termite mounds a useful and necessary feature to stabilize and increase the robustness of ecosystems (Bonachela *et al.*, 2015).

# CHAPTER 6 – DISCUSSION

Nests of the southern harvester termite (*Microhodotermes viator*) are hardened subterranean hives with extensive tunnel systems. These nests are described in detail from both intact nests and nest exposed by erosion in Clanwilliam (Moore and Picker, 1991). Recent work by McAuliffe *et al*. (2019) identified different manifestations of these nests, among which including sand-capped mounds on top of *M. viator* nests known as heuweltjies. Heuweltjies are described as raised mounds (< 2 m high) between 4-32 m in diameter (Lovegrove, 1991; Milton *et al.*, 1992) that occur in the south-western parts of the Succulent Karoo in South Africa (Lovegrove and Siegfried, 1989). However, earlier literature on *M. viator* did not make this distinction between heuweltjies and *M. viator* mounds (Coaton, 1958; Coaton and Sheasby, 1974). The confusing addition of the term "*heuweltjie*" and their defined distribution (Cramer and Midgley, 2015; Cramer *et al.*, 2017) long after the initial report for the distribution of *M. viator* (Coaton and Sheasby, 1974) have introduced confusion to the debate on heuweltjie origins.

## 6.1. Support for a termite heuweltjie origin

Of the several theories for the origin of heuweltjies (van der Merwe, 1944; Lovegrove and Siegfried, 1986) only two have withstood the test of time. The termite model, initially proposed by (Moore and Picker, 1991) has been supported through various lines of evidence (Picker *et al.*, 2007; McAuliffe *et al.*, 2019). The plant model for heuweltjie origin (Cramer *et al*. 2012) hypothesises that bush-clumps that originate as a result of nutrient patches within a landscape were responsible for their formation by which denser vegetation acts as an aeolian sediment trap, accumulating into mounds over time. McAuliffe *et al*. (2019) presented a system dynamics model that explains the formation of heuweltjies following the establishment of "*islands of fertility*" through actions of *M. viator*, however, the debate of origin remains contentious.

Coaton and Sheasby's (1974) distribution of the southern harvester termite spans winter and summer rainfall areas. After establishment of a strong association of *M. viator* with heuweltjies (Lovegrove and Siegfried 1986, 1989; Milton and Dean, 1990), Moore and Picker (1990) proposed that activity by *M. viator* was responsible for heuweltjies formation. Cramer and Midgley (2015) presented the incomplete spatial match of heuweltjies (Lovegrove and Siegfried, 1986; Midgley *et al.*, 2002) and *M. viator* (Coaton and Sheasby, 1974) as evidence against the termite theory in favour of the bush-clump theory (Cramer *et al.*, 2012). McAuliffe *et al*. (2018a) first described the different manifestations of *M. viator* nests either as nests without emergent structures, cemented conical mounds with or without remnants of a sand-capping or as sand-capped mounds known as heuweltjies. Their findings were interpreted in the context of heuweltjie genesis and identified different environmental variables (climate and sediment supply) as determinants for the manifestation of heuweltjies as opposed to nests with no emergent structures, or conical mounds (McAuliffe *et al.*, 2019). The different distribution of different manifestations of *M. viator* nests within the species distribution accounts for the perceived disjunct distribution of heuweltjies and *M. viator* (Cramer and Midgley, 2015). One of the remote sites identified in this study (Chapter 2) found heuweltjies further east than has previously been considered (Cramer and Midgley, 2015) but still within the range of *M. viator* distribution (Coaton and Sheasby, 1974).

The bush-clump theory states that mound soils are comparatively more enriched than matrix soils due to higher vegetation density and subsequent decomposition of plant litter (Cramer *et al.*, 2012). In addition, this theory stated that higher nutrient contents on heuweltjies compared to associated matrices was the result of greater nutrient leaching in the nutrient-poor matrix compared to nutrient-rich heuweltjie soils (Cramer *et al.*, 2016). This is contradictory to vegetation patch dynamics of spotted or "*leopard*" vegetation patches associated with fine-particle soil mounds, of which dynamics resemble that proposed by the bush-clump theory, that typically have greater water-infiltration rates on mounds compared to matrix habitats (Aguiar and Sala, 1999). In addition, water infiltration rates in heuweltjie soils was approximately five times faster than in matrix soils (Chapter 3), consistent with physical soil modifications by other termite species (Lee and Wood, 1971a; Kaiser *et al.*, 2017; Muvengwi, 2017; Govorushko, 2019). Cramer and Midgley (2015) argued that the presence of *M. viator* on heuweltjies was due to attraction of termites to the higher plant densities that result from enrichment of decaying plant matter.

Alternatively, the termite theory holds that soil nutrient enrichment typical of heuweltjies is primarily a result of termite faecal matter (frass) production, augmented by decomposition of stored plant material, and termite mortality (Matsumoto, 1976; Moore and Picker, 1991; Dangerfield *et al.*, 1998). The nature of heuweltjie soils enrichment (Chapter 3 of this thesis) parallels that of termite-enriched soils elsewhere (Nutting *et al.*, 1987; López-Hernández, 2001; Ndiaye *et al.*, 2004; Abe *et al.*, 2011; Tilahun *et al.*, 2012; Seymour *et al.*, 2014). This has been demonstrated to increase vegetation density (Bloesch, 2008; McAuliffe *et al.*, 2014; Anderson *et al.*, 2016). Cramer *et al*. (2012) cast doubt on the termite theory due to a lack of observed calcic soil horizons in some heuweltjies investigated in Clanwilliam, however, McAuliffe *et al*. (2014) recognized that the formation of such horizons is time-dependent (Gile *et al.*, 1966; McFadden and Tinsley, 1985) and could therefore be considered simply a matter of heuweltjie-age, rather than the absence of termites, which are known to accumulate calcium for the formation of such horizons (Ellis, 2002; Francis *et al.*, 2013), during heuweltjie formation.

The degree of carbon, calcium and nitrogen enrichment from surface deposits of *M. viator* frass in Worcester (476 kg per mound), exceeds that expected from the decomposition of plant detritus in denser vegetation i.e. bush-clumps (Schlesinger *et al.*, 1996; Jarvel and O'Connor, 1999; Escudero *et al.*, 2004; Abanda *et al.*, 2011; Cramer *et al.*, 2012; Cramer and Midgley, 2015; Getzin *et al.*, 2015b). Greater *in situ* water-infiltration was found in *M. viator* nest soils compared to matrix soils, and nutrient-profiles of nest soils represent a transition state between that of matrix soils and frass (Chapter 4). These results provide further support for the *M. viator* origin of heuweltjies.

## 6.2. Over-dispersion of heuweltjies

Cramer and Midgley (2015) compared evidence of bush-clump and termite origins of heuweltjies, stating that *M. viator* has no association with either winter rainfall or strong winds, which are consistent with the bush-clump theory which earlier suggested formation through differential erosion (Cramer *et al.*, 2012), but later suggested aeolian sediment accretion (Cramer *et al.*, 2016). However, heuweltjie (considered sand-capped nests of *M. viator*) distribution is only part of the total distribution of *M. viator* (Coaton and Sheasby, 1974; McAuliffe *et al*. 2019; 2018a), the remaining area covered by different manifestations of *M. viator* nests. Cramer and Midgley, 2015also argued that *M. viator* density decreases with aridity (Cramer and Midgley, 2015). However, Picker *et al*. (2007) found no overall relationship between density and rainfall of all sites (including high-rainfall Fynbos, and low-rainfall Karoo sites), but did find a positive relationship between rainfall and density when high-rainfall sites were removed from the model. They concluded that *M. viator* density is indirectly related to rainfall/aridity in combination with several other variables (vegetation type, soil type, and productivity). In this study, however, no relationship was found between density with rainfall at all sites, or separately in the Fynbos, Succulent Karoo or Albany thicket biomes (Chapter 2), contrary to the comparison made by Cramer and Midgley (2015).

Cramer and Midgley (2015) also argued that there was no evidence that *M. viator* colonies were over-dispersed, and that heuweltjie dispersion in hexagonal lattices is the result of spatial self-organization of bush-clumps as a result of plant-soil feedback between competitive and facilitative interactions and secondary habitation by *M. viator* (Bonami *et al.*, 2008; Rietkerk and Van de Koppel, 2008). However, there is evidence for the over-dispersion of *M. viator* colonies (McAuliffe *et al.*, 2018a) which is comparable to dispersion patterns of several other termite species (Getzin *et al.*, 2015a; Juergens *et al.*, 2015). This is further support for a termite origin of the heuwelties. However, considering that heuweltjie distribution is only part of the total distribution of *M. viator*, the remaining area represents the different manifestations of *M. viator* nests, which have been demonstrated to have similar dispersion patterns as heuweltjies (McAuliffe *et al*. 2019; 2018a).

Given the nature of termites as ecosystem engineers (Jones *et al.*, 1994; Dangerfield *et al.*, 1998; McAuliffe *et al.*, 2019) enriching soils in local landscapes and improving productivity, termite nest density and dispersion has been linked with optimal ecosystem function. Nests of *Odontotermes* sp. in Kenya, based on both field observations (Palmer, 2003; Brody *et al.*, 2010) and remote-sensing data (De La Maza *et al.*, 2009), were found to have greater primary productivity than the associated matrix and improved local diveristy (Pringle *et al.*, 2010). The resulting models found that the greatest net outcome of productivity was subject to regular pattern formation, or over-dispersion. It was reasonable to assume the same principles would apply to *M. viator*, however, the first attempts to quantify and compare the productivity (NDVI) of *M. viator* nests with the associated matrices, and between high- with low-densities of nests, did not find any relationships for the various vegetation types (Chapter 2).

### 6.3. Heuweltjie ontogeny

It is likely that nutrient build-up on heuweltjies, together with soil modification is a gradual process, and that only after some time will this be expressed in unique heuweltjie vegetation cover. Chapter 3). This is especially relevant given the estimated ages of living heuweltjies of 4000 years (Moore and Picker, 1991; Midgley *et al.*, 2002), Identifying a range of different aged heuweltjies and assessing the association with *M. viator* and plant density across ages could prove once and for all the origins of heuweltjies.

If the termite theory is correct, nascent heuweltjies present as one of the alternative manifestations of *M. viator* nests, either as cemented conical mounds or subterranean nests with no emergent structures (McAuliffe *et al.*, 2018a; McAuliffe *et al.*, 2019). Especially since senescence of heuweltjies has been observed following both natural death and death by poisoning of associated *M. viator* (Coaton, 1958; Milton and Dean, 1990). According to the genesis of heuweltjies, as proposed by McAuliffe *et al*. (2019), certain climatic criteria must be met to facilitate aeolian sediment accretion. Identifying sites of relatively young heuweltjies and following accretion data with increasing diameter of mounds/young nests would provide further insights on heuweltjie development. Alternatively, the association with *M. viator* and plant density can be assessed where the climatic criteria are met and known to have different manifestations of *M viator* nests.

Understanding and mapping the processes and interactions involved during early stages of heuweltjie development (Werner and Gilliam, 1984) would prove invaluable in anticipating reactions to changes in the environment (Yang and Rudolf, 2010; Pettorelli *et al.*, 2011)

### 6.4. Development of distinctive heuweltjie plant communities

Enrichment of heuweltjie soils has often been associated with distinct plant communities compared to the associated matrix in different regions (Midgley and Musil, 1990; Esler and Cowling, 1995; Luther-Mosebach *et al.*, 2012), however, aside from increased plant density few studies have explored the mechanisms by which these communities develop, or how certain species are selected or excluded from growing on heuweltjies. One of the drivers which have received some attention is the effect of disturbance. Heuweltjies are considered "*hotspots of disturbance*" (Esler and Cowling, 1995) attracting a variety of large herbivorous, fossorial rodents, and termite-predators such as aardvark (*Orycteropus afer*), the latter which also prefer the deeper (less consolidated) soils of heuweltjies to make their dens (Knight *et al.*, 1989; Milton and Dean, 1990; Esler and Cowling, 1995; Kunz *et al.*, 2012). Digging by mammals contributes to seed capture and through bioturbation improve soil conditions for favourable seedling germination and establishment (Gutterman *et al.*, 1990; Dean and Milton, 1991; Milton and Dean, 2015; Louw *et al.*, 2017).

Schmiedel *et al*. (2016) explored the effects of disturbance in the form of grazing influences on plant communities (life-form composition and diversity) on and between heuweltjies in the Succulent Karoo, which previously has been described in terms of decrease in perennial plant cover due to selective grazing (Todd and Hoffman, 1999). They found that species richness and diversity had a general increase from the matrix to the central parts of heuweltjies across grazing treatments. They found that vegetation dynamics on the fringe of heuweltjies (as opposed to central parts of heuweltjies and matrices) had the most distinct responses to grazing, and determined that duration and intensity of grazing modulate these responses.

Esler and Cowling (2005) investigated the life-history characteristics of several species of the Aizoaceae family, some of which occur predominantly on heuweltjies, and some which occur predominantly in the matrix. They found that matrix-species had greater germination success in experimental laboratory petri-dishes and lower seed retention than heuweltjie species. They conclude that these different life-history characteristics contribute to the selection/exclusion of species based on disturbance and competitive advantage, however, discounted these effects as adaptive to higher nutrient levels on heuweltjies since many of the species used in the heuweltjie treatment also occurred in the matrix. In Chapter 4 I provided evidence that seedling germination and survival in some species, as a factor of soil type (matrix of heuweltjie) potentially plays a considerable role in the selection/exclusion mechanisms that ultimately define and distinguish plant communities on heuweltjies from that of their associated matrices.

However, observations of two species of *Pteronia* spp. with presumably similar life-history characteristics growing together in Worcester (Rahlao *et al.*, 2008) – one occurring exclusively in the matrix (*P. paniculata*) and one exclusively on heuweltjies (*P. incana*) – suggested the existence of additional mechanisms differential survival driven by physical and/or chemical differences in soils. I found that both species had higher germination success in heuweltjie than matrix soils, however, *in situ* reciprocally transplanted seedlings of *P. paniculata* had greater qualitative health and root tolerance to transplant shock in native matrix habitats, and the latter was true for roots of *P. incana* in native heuweltjie soils. These results also provide evidence of a selection/exclusion mechanism driven by physical and/or chemical soil differences between matrix and heuweltjie habitats (Chapter 4). In addition, in the absence of termites, distinct vegetation composition changes across edaphic gradients is achieved by competitive exclusion and/or disturbance as found in the Fynbos-Succulent Karoo interface where Fynbos species fared better in reciprocal transplant trials than did Succulent Karoo counterparts (Esler *et al.*, 2015). These cumulative data suggest a complex species-specific response to different soil variables.

### 6.5. Ecosystem services provided by *M. viator*

Jouquet *et al*. (2011) discuss the general beneficial influences of termites on ecosystem functioning in terms of the decomposition of plant detritus, nutrient cycling, bioturbation and translocation of soils, soil-water properties, and local productivity and diversity.

*M. viator* forage preferably for short (<10 mm) cut pieces of woody plant stems which eventually enter the soil nutrient cycle in the form of frass (Picker *et al.*, 2004; Picker *et al.*, 2007; McAuliffe *et al.*, 2018a). The comparative nutrient profile of heuweltjie soils in Worcester (Chapter 4) was found to be intermediate between frass and the associated matrix soils. Heuweltjie nutrient profiles from several sites had higher concentrations of carbon, calcium and nitrogen than their associated matrices (Chapter 3) in addition to being comparable to nutrient profiles of heuweltjies in previous studies (Midgley and Musil, 1990; Kunz *et al.*, 2012) as well as other termites (Nutting *et al.*, 1987; López-Hernández, 2001; Ndiaye *et al.*, 2004; Abe *et al.*, 2011; Tilahun *et al.*, 2012; Seymour *et al.*, 2014).

Bioturbation of heuweltjies is brought about by the activity of *M. viator*, but also fossorial rodents and aardvark that are attracted to them (Milton and Dean, 1990; McAuliffe *et al*. 2014, 2018; Louw *et al*. 2017). Translocation of soil particles in the construction and maintenance of termite nests are widely reported and so mixes in frass to contribute to soil fertility (Bagine, 1984; De Bruyn and Conacher, 1990; Abe *et al.*, 2012; Jouquet *et al.*, 2016), however, this thesis did not find any difference in mean soil particle size in the topmost 15 cm of heuweltjie soils and their associated matrices, however, heuweltjies had much shorter water infiltration and longer water retention times (Chapter 4),.

The improved nutrient and soil water status of heuweltjies facilitate the development of denser and distinctive plant communities (Rahlao *et al.*, 2008; Luther-Mosebach *et al.*, 2012) with distinct faunal interactions (Milton and Dean, 1990; Louw *et al.*, 2017; Henschel and Lubin, 2018). Although no difference in productivity (measured as NDVI) was found between heuweltjies and their associated matrices (Chapter 2), however, several sites had greater plant density on heuweltjies compared to their associated matrices (Chapter 5). Plant density had a positive linear relationship with ant abundance demonstrating an influence on secondary consumers/predators. This influence potentially extends to other higher trophic levels, as Henschel and Lubin (2018) found greater abundances of web spiders on heuweltjies and state that this was possibly due to more favourable conditions there (described as greater protection, increased architectural space for webs, and greater abundance of herbivorous prey insects). Although no difference was found between diversity of ants on heuweltjies and their associated matrices, the presence of heuweltjies increased the local richness of both plant and ant species and a positive relationship was found between ant abundance and plant cover (Chapter 5).

Several theoretical mechanisms exist to explain ecosystem stability in terms of species diversity and richness, however, they remain equivocal (Cottingham *et al.*, 2001; Griffin *et al.*, 2009; Loreau and De Mazancourt, 2013). Most of these theories require a temporal account of fluctuations in species richness, diversity and evenness in combination with an understanding of each species' respective response to changes in the ecosystem to compensate for and buffer the effects of these changes on one another (McNaughton, 1977; Walker, 1992; Naeem and Li, 1997; Doak *et al.*, 1998; Tilman *et al.*, 1998; Ives *et al.*, 1999; Yachi and Loreau, 1999; Lavorel and Garnier, 2002)

## 6.6. Conclusion

McAuliffe *et al*. (2019) presented a system dynamics model explaining the genesis of sand-capped nests of *Microhodotermes viator*. This study supports the ecological assumptions used to develop this model and additionally contributes to a spatial dynamics component to the model (Figure 6.1) for which the steps as indicated in the figure are described here:

The original model starts with the colonization (**1**) and persistence (**2**) of *M. viator* in favourable habitats (Picker *et al.*, 2004). The influence of the colony on (**2.1**) initial soil conditions (**3**) enriches the soil and improves soil-water properties (See Chapters 3 and 4). New soil conditions (**4**) improve the growth and resilience of plants and thereby their density, while at the same time (**4.1**) introducing selective pressures that increase floral species richness and influence diversity (See Chapters 4 and 5). The subsequent increase in density and improved foliar nutrients in forage (**4**) attract fauna as either a source of food or refugia (**5**) and could potentially increase both faunal (**6.1**) density and (**6.2**) diversity (Henschel and Lubin, 2018; Arena *et al*. 2020; Chapter 5). The former (**6.1**) also contributes to (**3**) modification of soil through trampling, digging and dung (Milton and Dean, 1990; Picker *et al.*, 2007). In addition, greater floral density acts as an (**5**) aeolian sediment trap under (**4.1**) certain climatic conditions, which contribute to the development of sand-capped mounds or heuweltjies (McAuliffe *et al*. 2014; 2019). If the colony occupying the heuweltjie (**5**) succumbs to predation or becomes vacant for whatever reason, it is possible and given the proven quality of habitat, and density of overdispersed colonies, that it is very likely to be (**2**) secondarily inhabited by another *M. viator* colony (McGlynn, 2012). Increased plant density (**4**) also increases local productivity (**7**), which in turn attracts new colonies (**1**), which in turn contribute to further improving local productivity (**4** and **5**). The continued increase of nest density in response to productivity, and subsequent contribution of the former to productivity will ultimately reach an equilbirum of optimal carrying capacity (Begon *et al.*, 2006) resulting in the over-dispersion of long-lived persistent colonies (**8**) – a mechanism also subject to heterogeneity of biotic and abiotic variables itself (Laurie, 2002) but represents a relatively optimal degree of equilibrium between *M. viator* density and productivity when nearest neighbour densities are smallest. This state of (**8**) over-dispersion, in combination with increased (**4.1**) floral and (**6.2**) faunal diversity, contribute positively to the (**9**) stability of ecosystems (Cottingham *et al.*, 2001; Lavorel and Garnier, 2002; Hooper *et al.*, 2005; Pringle *et al.*, 2010).

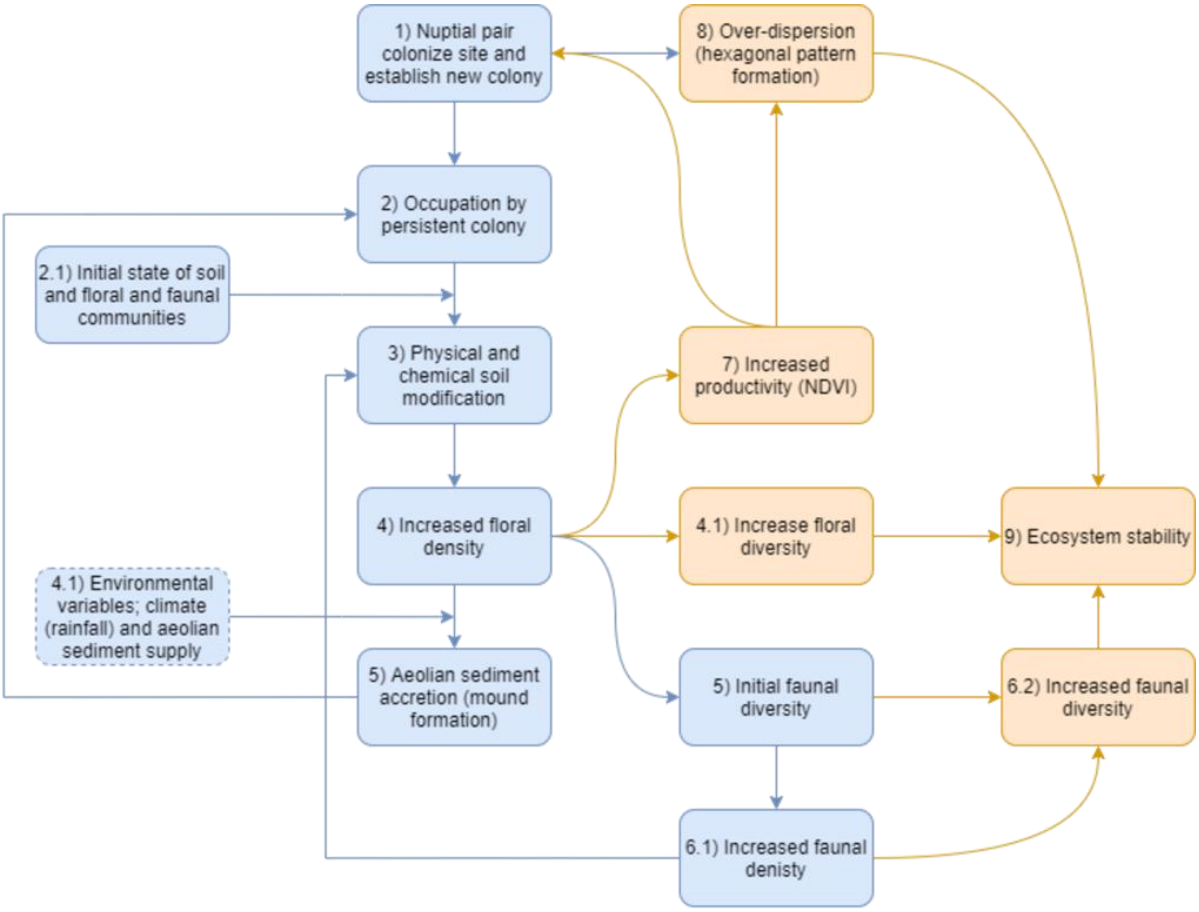

**Figure 6.8.** Building on the system dynamics model for the genesis of sand-capped *Microhodotermes viator* nests (heuweltjies) proposed by McAuliffe *et al*. (2019) in blue, with contributions to the spatial dynamics of nests and their influence on ecosystem diversity and stability determined from this study in orange.

In conclusion, the results presented in this thesis re-confirm several lines of evidence supporting the mechanism of heuweltjie genesis by the southern harvester termite (*M. viator*) (McAuliffe *et al.*, 2019), in addition to comparing nutrient profiles of frass, heuweltjie and matrix soils, and plant litter to find the latter is unable to generate the degree of enrichment observed on heuweltjies (Chapter 3). Chapter 4 provided further evidence that selective seedling germination, growth, and resilience, in addition to disturbance as known from literature (Schmiedel *et al.*, 2016), are components of a complex mechanism that distinguish plant communities between heuweltjies and their associated matrices (Esler, 1993; Milton, 1995). Over-dispersion of heuweltjies was detected in both high and low-density sites, and unlike Picker *et al*. (2007) no relationship was found between heuweltjie density and rainfall in any vegetation type. However, heuweltjie density had a positive relationship with productivity (Chapter 2). As expected, greater plant densities were found on heuweltjies compared to their associated matrices (Lovegrove, 1991; Rahlao *et al.*, 2008; Luther-

Mosebach *et al.*, 2012), and ant abundance had a positive relationship with plant density despite not being different between heuweltjies and matrices (Chapter 5). The presence of heuweltjies, however, increased species richness of both plants and ants (Lovegrove, 1991; Rahlao *et al.*, 2008; Arena *et al.*, 2020). Cumulatively these results in relation to ecosystem productivity (Pringle *et al.*, 2010) and species richness and diversity (Cottingham *et al.*, 2001; Hooper *et al.*, 2005) illustrate the importance of *M. viator* to ecosystem stability, and thus highlight the importance in conserving these structure to provide these important ecosystem services in light of inevitable climate change. The changes in amount and distribution of resources associated with *M. viator* make it an important ecosystem engineer (Dangerfield *et al.*, 1998; McAuliffe *et al.*, 2019), and by so doing increase the floral and faunal density and diversity also awarding it the title of keystone species (Redford, 1984; Mills *et al.*, 1993; Muvengwi and Witkowski, 2020).

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# APPENDICES

# Appendix A

The following extensive table presents the latitude and longitude of every plot, density of *M. viator* nests, mean nearest-neighbour distance (m), R-dispersion coefficient, percentage of hexagons from the two-dimensional Voronoi tessellation, mean nest diameter (m), vegetation classifications (biome, bioregion, and vegetation unit) according to Mucina and Rutherford (2006), mean annual precipitation (MAP, mm) from available values within the range 2006 – 2018, mean annual productivity as normalized difference vegetation indices (NDVI) of each plot, the matrix and the nests within plots, from three datasets (SPOT old and new, and MODIS). Mean rainfall determined between 2010 – 2017 is marked with a single asterisk (*), 2012 – 2017 with two (**), 2014 – 2017 with three (***), and between 2006 – 2018 with four (****).

| Site | Density | Nearest neighbour distance (m) | R-dispersion coefficient | Percentage hexagons | Diameter (m) | Biome | Bioregion | Vegetation unit |
|---|---|---|---|---|---|---|---|---|
| **1H** | 567 | 32,07 | 1,0511 | 37,64 | 30,93 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **1L** | 201 | 49,99 | 1,2173 | 35,33 | 29,95 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **2H** | 403 | 38,43 | 1,3339 | 38,57 | 33,74 | Succulent Karoo | Namaqualand Sandveld/Namaqualand Hardeveld | Namaqualand standveld/Namaqualand heulwetjieveld (SKs7/SKn4) |
| **2L** | 202 | 48,37 | 1,2429 | 26,74 | 33,32 | Succulent Karoo | Namaqualand Hardeveld/Namaqualand Sandveld | Namaqualand heuweltjieveld/Namaqualand strandveld (SKn4/SKs7) |
| **3H** | 277 | 44,90 | 1,2754 | 43,50 | 32,71 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand klipkoppe shrubland (SKn1) |
| **3L** | 97 | 54,97 | 1,1314 | 29,73 | 30,91 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand klipkoppe shrubland (SKn1) |
| **4H** | 308 | 40,74 | 1,2610 | 36,80 | 31,05 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **4L** | 189 | 48,11 | 1,1191 | 34,16 | 30,29 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **5H** | 341 | 41,31 | 1,2188 | 42,30 | 31,29 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld/Namaqualand klipkoppe shrubland (SKn4/SKn1) |
| **5L** | 118 | 63,47 | 1,3486 | 40,22 | 28,17 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **6H** | 338 | 40,90 | 1,2348 | 41,28 | 27,73 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **6L** | 193 | 46,74 | 1,3079 | 32,90 | 32,36 | Succulent Karoo | Namaqualand Hardeveld | Namaqualand heuweltjieveld (SKn4) |
| **7H** | 241 | 46,30 | 1,1792 | 33,67 | 44,25 | Succulent Karoo | Knersvlakte | Knersvlakte shale vygieveld (SKk4) |
| **7L** | 93 | 68,04 | 0,9510 | 24,62 | 22,41 | Succulent Karoo | Knersvlakte | Knersvlakte shale vygieveld (SKk4) |

| Site | Density | Nearest neighbour distance (m) | R-dispersion coefficient | Percentage hexagons | Diameter (m) | Biome | Bioregion | Vegetation unit |
|---|---|---|---|---|---|---|---|---|
| **8H** | 485 | 35,22 | 1,1672 | 40,54 | 24,25 | Succulent Karoo/Fynbos | Knersvlakte | Vanrhynsdorp gannabosveld (SKk5) |
| **8L** | 225 | 41,86 | 0,9486 | 37,17 | 21,82 | Succulent Karoo/Fynbos | Knersvlakte | Vanrhynsdorp gannabosveld/Knersvlakte dolomite vygieveld (SKk5/SKk6) |
| **9H** | 307 | 45,55 | 1,1889 | 39,11 | 20,30 | Succulent Karoo | Rainshadow Valley Karoo | Tanqua karoo (SKv5) |
| **9L** | 194 | 55,81 | 1,2986 | 39,75 | 26,87 | Succulent Karoo | Rainshadow Valley Karoo | Tanqua karoo (SKv5) |
| **10H** | 323 | 40,65 | 1,1931 | 39,22 | 27,79 | Fynbos | Shale Renosterveld | Swartland shale renosterveld (FRs9) |
| **10L** | 144 | 45,74 | 0,8794 | 30,43 | 24,64 | Fynbos | Shale Renosterveld | Swartland shale renosterveld (FRs9) |
| **11H** | 335 | 40,90 | 1,2114 | 36,73 | 21,50 | Succulent Karoo | Rainshadow Valley Karoo | Tanqua karoo (SKv5) |
| **11L** | 210 | 44,63 | 1,0835 | 34,09 | 23,93 | Succulent Karoo | Rainshadow Valley Karoo | Tanqua karoo (SKv5) |
| **12H** | 221 | 44,17 | 0,4385 | 37,11 | 23,09 | Fynbos | Granite Fynbos/Sandstone Fynbos/Shale Fynbos | Boland granite fynbos/Bokkeveld sandstone fynbos/Cape winelands shale fynbos (FFg2/FFs1/FFh5) |
| **12L** | 88 | 42,82 | 0,5204 | 34,85 | 26,69 | Fynbos | Granite Fynbos/Sandstone Fynbos | Boland granite fynbos/Bokkeveld sandstone fynbos (FFg2/FFs1 ) |
| **13H** | 188 | 49,36 | 0,9425 | 35,57 | 28,24 | Succulent Karoo/Fynbos | Rainshadow Valley Karoo/Shale Renosterveld | Robertson karoo/Matjiesfontein shale renosterveld (SKv7/FRs6) |
| **13L** | 217 | 55,39 | 1,00 | 28,69 | 28,02 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **14H** | 337 | 38,09 | 1,1495 | 33,67 | 33,35 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **14L** | 82 | 66,00 | 0,9940 | 35,94 | 25,82 | Succulent Karoo/Fynbos | Rainshadow Valley Karoo/Quartzite Fynbos | Robertson karoo/Breede quartzite fynbos (SKv7/FFq4) |
| **15H** | 443 | 34,13 | 1,1880 | 42,47 | 26,62 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **15L** | 150 | 53,10 | 1,1513 | 25,62 | 23,76 | Fynbos | Sand Fynbos | Knysna sand fynbos (FFd10) |
| **16H** | 294 | 39,56 | 1,0257 | 39,53 | 25,38 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **16L** | 172 | 47,02 | 0,7247 | 32,12 | 23,05 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **17H** | 289 | 41,79 | 1,1150 | 36,25 | 20,43 | Succulent Karoo/Fynbos | Rainshadow Valley Karoo/Shale Renosterveld | Koedoesberge moordenaars karoo/Matjiesfontein shale renosterveld (SKv6/FRs6) |
| **17L** | 82 | 56,90 | 1,0092 | 41,67 | 22,88 | Fynbos | Shale Renosterveld/Quartzite Fynbos | Matjiesfontein shale renosterveld/Matjiesfontein quartzite fynbos (FRs6/FFq3) |
| **18H** | 169 | 55,49 | 1,0539 | 31,88 | 19,69 | Succulent Karoo | Rainshadow Valley Karoo | Koedoesberge moordernaars karoo (SKv6 ) |

| Site | Density | Nearest neighbour distance (m) | R-dispersion coefficient | Percentage hexagons | Diameter (m) | Biome | Bioregion | Vegetation unit |
|---|---|---|---|---|---|---|---|---|
| **18L** | 95 | 67,96 | 1,2106 | 28,57 | 17,50 | Succulent Karoo | Rainshadow Valley Karoo | Koedoesberge moordernaars karoo (SKv6 ) |
| **19H** | 329 | 36,79 | 1,1788 | 34,56 | 20,57 | Succulent Karoo | Rainshadow Valley Karoo | Western little karoo/Little karoo quartz vygieveld (SKv8/SKv10) |
| **19L** | 118 | 52,82 | 1,1092 | 32,26 | 20,48 | Succulent Karoo | Rainshadow Valley Karoo | Western little karoo (SKv8 ) |
| **20H** | 377 | 34,03 | 0,9244 | 33,33 | 18,15 | Succulent Karoo | Inland Saline Vegetation | Southern karoo riviere (AZi6) |
| **20L** | 258 | 38,09 | 1,0154 | 37,95 | 15,96 | Succulent Karoo | Inland Saline Vegetation | Southern karoo riviere (AZi6) |
| **21H** | 457 | 33,80 | 1,3398 | 37,50 | 13,85 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **21L** | 237 | 43,78 | 1,2153 | 38,19 | 19,95 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **22H** | 720 | 27,97 | 1,1397 | 41,21 | 26,50 | Albany Thicket | NA | Gamka thicket (AT2) |
| **22L** | 296 | 40,34 | 1,2874 | 35,32 | 19,64 | Albany Thicket | NA | Gamka thicket (AT2) |
| **23H** | 207 | 47,85 | 1,2592 | 36,00 | 19,68 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **23L** | 95 | 62,83 | 1,1391 | 32,43 | 15,57 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **24H** | 155 | 46,07 | 1,2558 | 29,03 | 19,58 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **24L** | 76 | 78,12 | 1,3134 | 40,00 | 23,15 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **25H** | 339 | 50,15 | 0,0385 | 35,76 | 20,95 | Albany Thicket | NA | Great bush thicket (AT11) |
| **25L** | 150 | 44,19 | 0,98 | 27,32 | 19,50 | Albany Thicket | NA | Great bush thicket (AT11) |
| **26H** | 208 | 44,32 | 0,8882 | 34,97 | 16,77 | Succulent Karoo | Rainshadow Valley Karoo | Agter Sederberg shrubland/Tanqua karoo (SKv3/SKv5) |
| **26L** | 160 | 42,60 | 0,9436 | 30,00 | 22,98 | Succulent Karoo | Rainshadow Valley Karoo | Agter Sederberg shrubland (SKv3 ) |
| **27H** | 158 | 43,20 | 1,0942 | 30,71 | 20,92 | Fynbos | Sandstone Fynbos | Winterhoek sandstone fynbos (FFs5) |
| **27L** | 152 | 47,43 | 0,9477 | 32,58 | 21,28 | Fynbos | Sandstone Fynbos | Winterhoek sandstone fynbos (FFs5) |
| **28H** | 190 | 40,69 | 0,9593 | 40,68 | 18,85 | Fynbos | Shale Fynbos/Shale Renosterveld | Breede shale fynbos/Breede shale renosterveld (FFh4/FRs8) |
| **28L** | 116 | 42,19 | 0,5474 | 33,33 | 21,74 | Fynbos | Shale Fynbos/Shale Renosterveld | Breede shale fynbos/Breede shale renosterveld (FFh4/FRs8) |
| **29H** | 143 | 53,57 | 1,1412 | 37,04 | 22,20 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **29L** | 74 | 74,08 | 1,0892 | 22,45 | 19,28 | Succulent Karoo | Rainshadow Valley Karoo | Prince Albert succulent karoo (SKv13) |
| **30H** | 165 | 46,30 | 1,1025 | 38,41 | 17,32 | Albany Thicket | NA /Inland Saline Vegetation | Groot thicket/Southern karoo riviere (AT3/AZi6) |

| Site | Density | Nearest neighbour distance (m) | R-dispersion coefficient | Percentage hexagons | Diameter (m) | Biome | Bioregion | Vegetation unit |
|---|---|---|---|---|---|---|---|---|
| **30L** | 121 | 51,74 | 1,0863 | 33,68 | 20,90 | Albany Thicket | NA /Inland Saline Vegetation | Groot thicket/Southern karoo riviere (AT3/AZi6) |
| **31H** | 436 | 33,64 | 1,1115 | 40,30 | 20,21 | Succulent Karoo | Knersvlakte | Citrusdal vygieveld (SKk7) |
| **31L** | 310 | 41,18 | 1,1343 | 47,46 | 25,18 | Succulent Karoo | Knersvlakte | Citrusdal vygieveld (SKk7) |
| **32H** | 166 | 48,56 | 1,0421 | 36,96 | 23,67 | Fynbos | Shale Renosterveld | Swartland shale renosterveld (FRs9) |
| **32L** | 193 | 46,89 | 1,0073 | 27,11 | 24,75 | Fynbos | Shale Renosterveld | Swartland shale renosterveld (FRs9) |
| **33H** | 310 | 38,75 | 1,0175 | 32,25 | 26,40 | Succulent Karoo | Rainshadow Valley Karoo/Allucium Renosterveld | Robertson karoo/Breede alluvium renosterveld (SKv7/FRa1) |
| **33L** | 97 | 60,49 | 0,8253 | 36,23 | 18,99 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **34H** | 219 | 42,14 | 0,9458 | 35,71 | 21,33 | Fynbos | Shale Renosterveld | Matjiesfontein shale renosterveld (FRs6) |
| **34L** | 156 | 54,30 | 1,3113 | 29,69 | 21,86 | Fynbos | Shale Renosterveld | Matjiesfontein shale renosterveld (FRs6) |
| **35H** | 146 | 55,50 | 1,0770 | 37,29 | 19,51 | Fynbos | Shale Renosterveld | Montagu shale renosterveld (FRs7) |
| **35L** | 117 | 64,54 | 1,2006 | 30,77 | 21,63 | Fynbos | Shale Renosterveld | Montagu shale renosterveld (FRs7) |
| **36H** | 294 | 39,92 | 1,0824 | 32,17 | 26,65 | Succulent Karoo | Rainshadow Valley Karoo | Little karoo quartz vygieveld (SKv10) |
| **36L** | 122 | 57,45 | 1,1739 | 26,09 | 21,53 | Fynbos/Succulent Karoo | Shale Renosterveld/Rainshadow Valley Karoo | Montagu shale renosterveld/Western little karoo (FRs7/SKv8) |
| **37H** | 579 | 29,42 | 1,0365 | 35,51 | 21,49 | Succulent Karoo | Rainshadow Valley Karoo | Eastern little karoo (SKv11) |
| **37L** | 324 | 35,95 | 1,0030 | 35,89 | 21,56 | Succulent Karoo | Rainshadow Valley Karoo | Eastern little karoo (SKv11) |
| **38H** | 220 | 43,33 | 0,9229 | 31,22 | 26,05 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |
| **38L** | 214 | 45,15 | 0,7485 | 30,86 | 23,41 | Succulent Karoo | Rainshadow Valley Karoo | Robertson karoo (SKv7) |

| Site | MAP | Site |  |  |  |  | Matrix |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) |
| **1H** | 90,75 * | 0,07680 | 0,20409 | 0,35913 | 0,20936 | 0,20763 | 0,07750 | 0,19727 | 0,35563 |
| **1L** | 90,75 * | 0,08061 | 0,21521 | 0,34157 | 0,21526 | 0,21067 | 0,07818 | 0,23680 | 0,34129 |
| **2H** | 90,75 * | 0,07334 | 0,26301 | 0,37157 | 0,21677 | 0,21051 | 0,07298 | 0,27543 | 0,38747 |

| Site | MAP | Site | | | | | Matrix | | |
|---|---|---|---|---|---|---|---|---|---|
| | | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) |
| **2L** | 90,75 * | 0,05315 | 0,25200 | 0,36349 | 0,19807 | 0,19487 | 0,05288 | 0,25332 | 0,36526 |
| **3H** | 196,27 ** | 0,14357 | 0,17487 | 0,30700 | 0,29114 | 0,29929 | 0,14030 | 0,17351 | 0,30498 |
| **3L** | 196,27 ** | 0,15304 | 0,19696 | 0,29583 | 0,27472 | 0,27547 | 0,15598 | 0,18294 | 0,28092 |
| **4H** | 123,49 * | 0,13139 | 0,22936 | 0,32723 | 0,21414 | 0,21696 | 0,13162 | 0,22462 | 0,32392 |
| **4L** | 123,49 * | 0,13948 | 0,21346 | 0,32825 | 0,20662 | 0,21592 | 0,13910 | 0,20655 | 0,32603 |
| **5H** | 196,27 ** | 0,14413 | 0,18780 | 0,29474 | 0,23029 | 0,22825 | 0,14645 | 0,18111 | 0,28963 |
| **5L** | 196,27 ** | 0,14173 | 0,22267 | 0,35094 | 0,21668 | 0,21381 | 0,14000 | 0,22497 | 0,35212 |
| **6H** | 123,49 * | 0,16477 | 0,24429 | 0,33809 | 0,22874 | 0,22983 | 0,16240 | 0,25791 | 0,34563 |
| **6L** | 123,49 * | 0,10231 | 0,25715 | 0,34322 | 0,24700 | 0,24479 | 0,09569 | 0,25777 | 0,34316 |
| **7H** | 162,88 * | 0,12557 | 0,29725 | 0,34805 | 0,17741 | 0,17392 | 0,12576 | 0,29993 | 0,35032 |
| **7L** | 162,88 * | 0,12355 | 0,30328 | 0,34970 | 0,16734 | 0,16470 | 0,12242 | 0,30350 | 0,34893 |
| **8H** | 162,88 * | 0,12882 | 0,25326 | 0,25853 | 0,25820 | 0,24954 | 0,13201 | 0,25350 | 0,25883 |
| **8L** | 162,88 * | 0,12047 | 0,33452 | 0,33570 | 0,21441 | 0,22898 | 0,11781 | 0,33670 | 0,34023 |
| **9H** | 201,63 * | 0,10784 | | 0,31478 | 0,21297 | 0,19372 | 0,10834 | | 0,31478 |
| **9L** | 201,63 * | 0,11204 | | 0,30236 | 0,20180 | 0,18911 | 0,11031 | | 0,30401 |
| **10H** | 348,63 * | 0,13366 | | | 0,38235 | 0,45008 | 0,12814 | | |
| **10L** | 348,63 * | 0,14970 | | | 0,35246 | 0,44838 | 0,15006 | | |
| **11H** | 777,65 *** | 0,10940 | | | 0,20880 | 0,18125 | 0,10914 | | |
| **11L** | 777,65 *** | 0,11425 | | | 0,19132 | 0,16863 | 0,11432 | | |
| **12H** | 1060,14 * | 0,08506 | | | 0,40087 | 0,44503 | 0,08586 | | |
| **12L** | 1060,14 * | 0,10785 | | | 0,46718 | 0,52614 | 0,10671 | | |
| **13H** | 285,78 **** | 0,07689 | | | 0,31447 | 0,28189 | 0,07169 | | |
| **13L** | 285,78 **** | 0,06755 | | | 0,30868 | 0,28085 | 0,06417 | | |
| **14H** | 285,78 **** | 0,11062 | | | 0,30761 | 0,29950 | 0,09962 | | |
| **14L** | 285,78 **** | 0,12998 | | | 0,27444 | 0,26796 | 0,12940 | | |
| **15H** | 319,70 * | 0,14885 | | | 0,32910 | 0,30961 | 0,15723 | | |

| Site | MAP | Site | | | | | Matrix | | |
|---|---|---|---|---|---|---|---|---|---|
| | | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) |
| **15L** | 319,70 * | 0,14695 | | | 0,27813 | 0,25721 | 0,14636 | | |
| **16H** | 319,70 * | 0,15237 | | | 0,30147 | 0,28816 | 0,15671 | | |
| **16L** | 319,70 * | 0,15697 | | | 0,29180 | 0,28784 | 0,15676 | | |
| **17H** | 115,75 * | 0,12899 | | | 0,20619 | 0,17985 | 0,12550 | | |
| **17L** | 115,75 * | 0,12682 | | | 0,22556 | 0,18343 | 0,12557 | | |
| **18H** | 115,75 * | 0,11809 | | | 0,17347 | 0,14280 | 0,12059 | | |
| **18L** | 115,75 * | 0,12591 | | | 0,16071 | 0,13028 | 0,12845 | | |
| **19H** | 332,53 * | 0,15225 | | | 0,19381 | 0,16265 | 0,15289 | | |
| **19L** | 332,53 * | 0,14492 | | | 0,17938 | 0,15345 | 0,14380 | | |
| **20H** | 144,45 * | 0,16180 | | | 0,19369 | 0,15960 | 0,16322 | | |
| **20L** | 144,45 * | 0,18461 | | | 0,14701 | 0,12403 | 0,18595 | | |
| **21H** | 144,45 * | 0,15046 | 0,11550 | 0,16637 | 0,17254 | 0,13388 | 0,15059 | 0,11335 | 0,16627 |
| **21L** | 144,45 * | 0,14641 | 0,10753 | 0,16534 | 0,16621 | 0,12912 | 0,14602 | 0,10651 | 0,16425 |
| **22H** | 244,73 * | 0,14312 | 0,14813 | 0,22131 | 0,39471 | 0,34680 | 0,14103 | 0,13381 | 0,17374 |
| **22L** | 244,73 * | 0,14810 | 0,11548 | | 0,44747 | 0,38458 | 0,14635 | 0,10992 | |
| **23H** | 144,45 * | 0,14169 | 0,08047 | 0,13378 | 0,16427 | 0,12276 | 0,14116 | 0,07386 | 0,12865 |
| **23L** | 144,45 * | 0,17454 | 0,05448 | 0,12439 | 0,16352 | 0,12110 | 0,17418 | 0,05644 | 0,12427 |
| **24H** | 282,23 * | 0,14440 | 0,06766 | 0,14563 | 0,12185 | 0,09428 | 0,14305 | 0,06766 | 0,14563 |
| **24L** | 282,23 * | 0,14022 | 0,06151 | 0,15106 | 0,13677 | 0,10278 | 0,13990 | 0,06342 | 0,15385 |
| **25H** | 555,93 * | 0,18507 | 0,07518 | 0,13964 | 0,30431 | 0,25827 | 0,18590 | 0,06247 | 0,12039 |
| **25L** | 555,93 * | 0,19001 | 0,12576 | 0,22685 | 0,40329 | 0,32710 | 0,19429 | 0,12352 | 0,20459 |
| **26H** | 201,63 * | 0,16035 | 0,15716 | 0,21420 | 0,19965 | 0,18461 | 0,16161 | 0,15619 | 0,21362 |
| **26L** | 201,63 * | 0,12130 | 0,16275 | 0,22242 | 0,20678 | 0,19035 | 0,12060 | 0,16275 | 0,22242 |
| **27H** | 353,85 * | 0,15958 | | | 0,44267 | 0,47461 | 0,15924 | | |
| **27L** | 353,85 * | 0,10367 | | | 0,49974 | 0,49829 | 0,10147 | | |
| **28H** | 777,65 *** | 0,14206 | | | 0,40614 | 0,42420 | 0,14590 | | |

| Site | MAP | | Site | | | | | Matrix | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) |
| **28L** | 777,65 | *** | 0,14126 | | | 0,34782 | 0,38714 | 0,14186 | | |
| **29H** | 282,23 | * | 0,11210 | 0,17215 | 0,24837 | 0,17093 | 0,13456 | 0,11158 | 0,16590 | 0,23999 |
| **29L** | 282,23 | * | 0,12108 | 0,02328 | 0,10676 | 0,13857 | 0,10737 | 0,12168 | 0,02362 | 0,10686 |
| **30H** | 282,23 | * | 0,18183 | 0,25148 | 0,31782 | 0,24901 | 0,19493 | 0,18285 | 0,25272 | 0,31820 |
| **30L** | 282,23 | * | 0,19977 | 0,21779 | 0,30064 | 0,25627 | 0,18495 | 0,19867 | 0,21779 | 0,30064 |
| **31H** | 182,20 | * | 0,06728 | 0,21453 | | 0,29455 | 0,33111 | 0,06291 | 0,21794 | |
| **31L** | 182,20 | * | 0,12232 | 0,24384 | | 0,25792 | 0,29167 | 0,12331 | 0,24452 | |
| **32H** | 359,10 | * | 0,11431 | | | 0,38042 | 0,46615 | 0,11119 | | |
| **32L** | 359,10 | * | 0,11039 | | | 0,34787 | 0,42125 | 0,10455 | | |
| **33H** | 285,78 | **** | 0,10864 | | | 0,31747 | 0,30719 | 0,11892 | | |
| **33L** | 285,78 | **** | 0,05673 | | | 0,34853 | 0,34414 | 0,05560 | | |
| **34H** | 319,70 | * | 0,14267 | | | 0,23881 | 0,21282 | 0,14271 | | |
| **34L** | 319,70 | * | 0,15273 | | | 0,18943 | 0,17461 | 0,15898 | | |
| **35H** | 700,70 | *** | 0,11838 | | | 0,18230 | 0,17040 | 0,11949 | | |
| **35L** | 700,70 | *** | 0,09397 | | | 0,19630 | 0,17968 | 0,09532 | | |
| **36H** | 332,53 | * | 0,13239 | | | 0,17072 | 0,15934 | 0,13486 | | |
| **36L** | 332,53 | * | 0,12115 | | | 0,18548 | 0,17523 | 0,11704 | | |
| **37H** | 244,73 | * | 0,12880 | | | 0,31220 | 0,27458 | 0,13390 | | |
| **37L** | 244,73 | * | 0,12851 | | | 0,35854 | 0,30375 | 0,12896 | | |
| **38H** | 285,78 | **** | 0,09739 | | | 0,33948 | 0,34015 | 0,09481 | | |
| **38L** | 285,78 | **** | 0,11233 | | | 0,33539 | 0,32551 | 0,11089 | | |

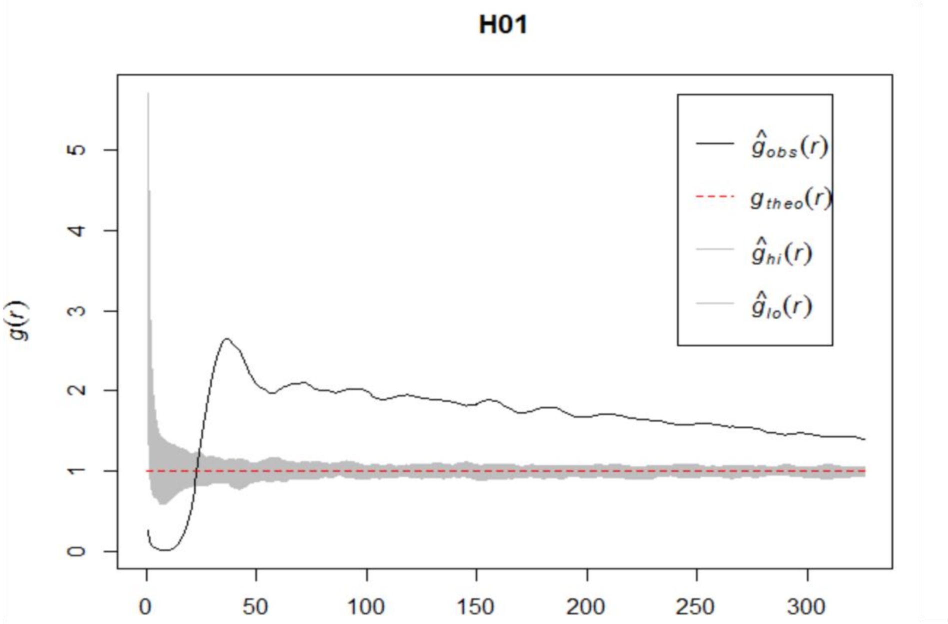
| Site | Matrix | | Nest | | | | | g(r) | r-distance |
|---|---|---|---|---|---|---|---|---|---|
| | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | | |
| **1H** | 0,20837 | 0,20715 | 0,07690 | 0,22329 | 0,37395 | 0,20949 | 0,20866 | 2,72618 | 36,91030 |
| **1L** | 0,21535 | 0,21077 | 0,10892 | 0,25073 | 0,36579 | 0,21604 | 0,21386 | 1,71959 | 58,48128 |
| **2H** | 0,21741 | 0,21070 | 0,06250 | 0,25316 | 0,35777 | 0,21606 | 0,21190 | 1,52670 | 54,26619 |
| **2L** | 0,19955 | 0,19592 | 0,04529 | 0,22796 | 0,34398 | 0,19730 | 0,19750 | 1,74150 | 50,52782 |
| **3H** | 0,28710 | 0,29541 | 0,15873 | 0,15567 | 0,29598 | 0,28637 | 0,29704 | 1,87091 | 52,77004 |
| **3L** | 0,27551 | 0,27533 | 0,11660 | 0,21072 | 0,32045 | 0,27346 | 0,27727 | 1,90914 | 61,03009 |
| **4H** | 0,21218 | 0,21595 | 0,12453 | 0,23374 | 0,33520 | 0,21515 | 0,21977 | 1,77109 | 82,97258 |
| **4L** | 0,20690 | 0,21579 | 0,13540 | 0,23463 | 0,34093 | 0,20720 | 0,21797 | 2,39288 | 59,24156 |
| **5H** | 0,23225 | 0,22970 | 0,13481 | 0,18917 | 0,30207 | 0,23174 | 0,23236 | 1,76051 | 56,30356 |
| **5L** | 0,21694 | 0,21386 | 0,20264 | 0,18997 | 0,31880 | 0,21681 | 0,21572 | 1,56945 | 68,46680 |
| **6H** | 0,22869 | 0,22940 | 0,16539 | 0,22185 | 0,31693 | 0,22794 | 0,23003 | 1,76270 | 52,17617 |
| **6L** | 0,24656 | 0,24466 | 0,13108 | 0,24544 | 0,33374 | 0,24422 | 0,24625 | 1,30828 | 73,88005 |
| **7H** | 0,17813 | 0,17453 | 0,12497 | 0,28653 | 0,33596 | 0,17794 | 0,17655 | 1,79112 | 48,69618 |
| **7L** | 0,16752 | 0,16480 | 0,11049 | 0,29323 | 0,33915 | 0,16610 | 0,16425 | 2,62284 | 70,55593 |
| **8H** | 0,25763 | 0,24950 | 0,11276 | 0,24491 | 0,25074 | 0,25792 | 0,25449 | 2,10226 | 42,26637 |
| **8L** | 0,21470 | 0,22829 | 0,12502 | 0,32252 | 0,32957 | 0,21373 | 0,23399 | 2,49027 | 43,56600 |
| **9H** | 0,21297 | 0,19372 | 0,10834 | | 0,30792 | 0,21410 | 0,19635 | 1,92444 | 55,60618 |
| **9L** | 0,20157 | 0,18900 | 0,12006 | | 0,30056 | 0,20243 | 0,19032 | 1,76806 | 67,07504 |
| **10H** | 0,38341 | 0,44894 | 0,15308 | | | 0,37557 | 0,44288 | 1,70607 | 56,26935 |
| **10L** | 0,35370 | 0,44805 | 0,16479 | | | 0,35374 | 0,44360 | 2,24905 | 46,43188 |
| **11H** | 0,20880 | 0,18125 | 0,11415 | | | 0,20921 | 0,18537 | 1,68973 | 66,06506 |
| **11L** | 0,19052 | 0,16808 | 0,09365 | | | 0,18821 | 0,16802 | 1,95670 | 62,18224 |
| **12H** | 0,40418 | 0,44882 | 0,07974 | | | 0,38585 | 0,42001 | 10,64556 | 54,15052 |
| **12L** | 0,43904 | 0,52581 | 0,12063 | | | 0,45804 | 0,50538 | 6,29619 | 50,38903 |
| **13H** | 0,31447 | 0,28189 | 0,10370 | | | 0,31950 | 0,28540 | 2,34557 | 82,75093 |
| **13L** | 0,31979 | 0,28069 | 0,07648 | | | 0,30912 | 0,28252 | 1,88330 | 60,91300 |

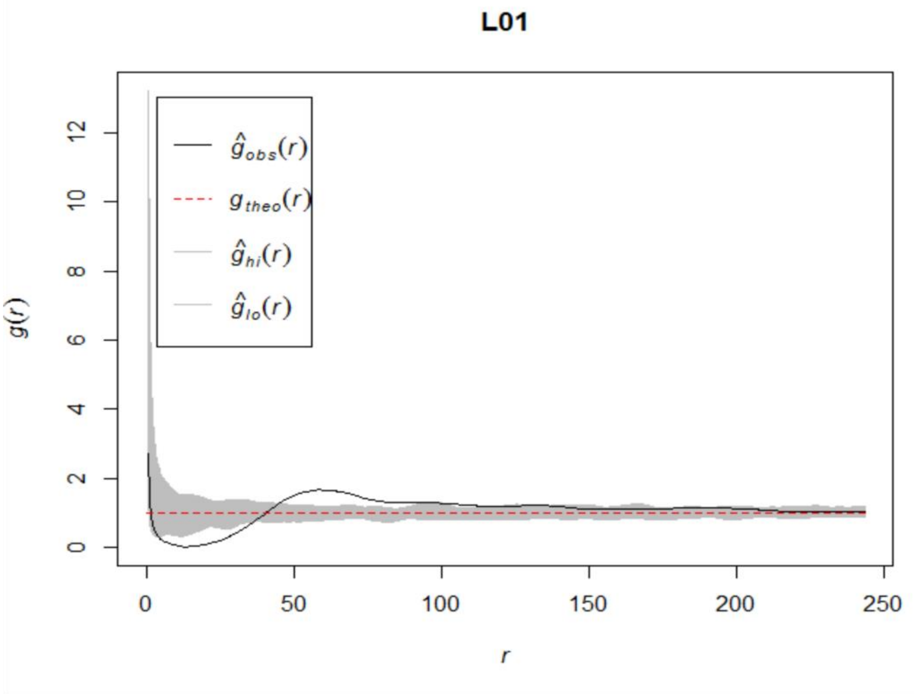
| Site | Matrix | | Nest | | | | | g(r) | r-distance |
|---|---|---|---|---|---|---|---|---|---|
| | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | | |
| **14H** | 0,30964 | 0,30160 | 0,09951 | | | 0,30690 | 0,30270 | 1,69668 | 42,17941 |
| **14L** | 0,27488 | 0,26832 | 0,14791 | | | 0,27649 | 0,27423 | 1,68031 | 44,19051 |
| **15H** | 0,33109 | 0,31029 | 0,11787 | | | 0,33580 | 0,32316 | 1,86193 | 39,18710 |
| **15L** | 0,27921 | 0,25803 | 0,12189 | | | 0,27958 | 0,26176 | 1,54440 | 107,36050 |
| **16H** | 0,30390 | 0,28971 | 0,13931 | | | 0,29765 | 0,28921 | 1,94243 | 51,91245 |
| **16L** | 0,28988 | 0,28737 | 0,17406 | | | 0,28828 | 0,28662 | 3,61319 | 50,16690 |
| **17H** | 0,20620 | 0,18018 | 0,18890 | | | 0,20135 | 0,17641 | 1,65706 | 68,57474 |
| **17L** | 0,22556 | 0,18343 | 0,18041 | | | 0,21473 | 0,17634 | 2,16851 | 60,40262 |
| **18H** | 0,17369 | 0,14272 | 0,04495 | | | 0,17389 | 0,14300 | 1,77739 | 64,17436 |
| **18L** | 0,16071 | 0,13028 | 0,09514 | | | 0,16219 | 0,13109 | 1,45201 | 101,72620 |
| **19H** | 0,19440 | 0,16315 | 0,14228 | | | 0,19418 | 0,16344 | 1,46430 | 47,12939 |
| **19L** | 0,17938 | 0,15345 | 0,20309 | | | 0,17913 | 0,15415 | 1,46833 | 62,02324 |
| **20H** | 0,19474 | 0,16114 | 0,13104 | | | 0,19216 | 0,16005 | 2,17540 | 36,61825 |
| **20L** | 0,14689 | 0,12368 | 0,13464 | | | 0,14774 | 0,12638 | 1,71559 | 64,80850 |
| **21H** | 0,17208 | 0,13346 | 0,15599 | 0,13301 | 0,17614 | 0,17322 | 0,13519 | 1,24844 | 46,51457 |
| **21L** | 0,16728 | 0,12947 | 0,22061 | 0,12683 | 0,17510 | 0,16164 | 0,12735 | 1,54067 | 55,82240 |
| **22H** | 0,39355 | 0,34454 | 0,14885 | 0,17147 | 0,22207 | 0,39213 | 0,34900 | 1,98403 | 38,92924 |
| **22L** | 0,45125 | 0,38771 | 0,15060 | 0,11924 | | 0,44483 | 0,38569 | 1,56011 | 48,87090 |
| **23H** | 0,16484 | 0,12288 | 0,15273 | | | 0,16464 | 0,12288 | 1,35914 | 76,43036 |
| **23L** | 0,16352 | 0,12110 | 0,17979 | 0,07396 | 0,14517 | 0,16383 | 0,12113 | 1,56151 | 104,34240 |
| **24H** | 0,12185 | 0,09428 | 0,15670 | 0,08567 | 0,16886 | 0,12424 | 0,09608 | 1,40174 | 86,57615 |
| **24L** | 0,13722 | 0,10272 | 0,16090 | 0,06980 | 0,15776 | 0,13416 | 0,10066 | 1,07699 | 83,91674 |
| **25H** | 0,31696 | 0,26812 | 0,17577 | 0,09922 | 0,19195 | 0,30155 | 0,24082 | 1,89713 | 66,59339 |
| **25L** | 0,40754 | 0,32942 | 0,16010 | 0,15935 | 0,27345 | 0,39921 | 0,30896 | 1,94732 | 40,84601 |
| **26H** | 0,19957 | 0,18442 | 0,13347 | | | 0,20036 | 0,18576 | 2,79330 | 52,00928 |
| **26L** | 0,20678 | 0,19035 | 0,13379 | 0,15570 | 0,22179 | 0,20861 | 0,19387 | 2,38523 | 40,52443 |

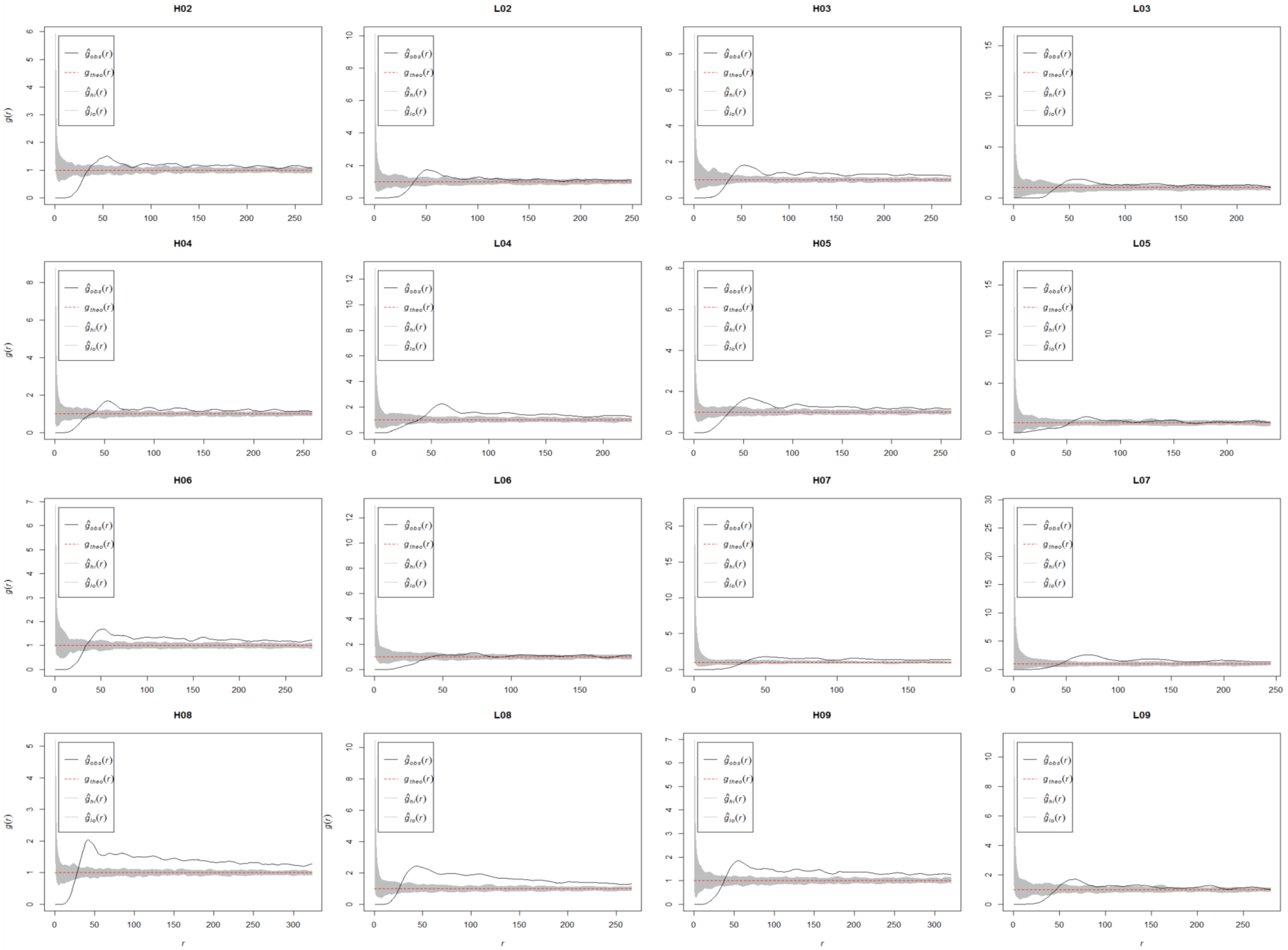
| Site | Matrix | | Nest | | | | | g(r) | r-distance |
|---|---|---|---|---|---|---|---|---|---|
| | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | NDVI (SPOT, autumn - old) | NDVI (SPOT, autumn - new) | NDVI (SPOT, spring - new) | NDVI (MODIS, autumn) | NDVI (MODIS, spring) | | |
| **27H** | 0,44607 | 0,47734 | 0,15089 | | | 0,42898 | 0,45825 | 2,34394 | 75,08138 |
| **27L** | 0,49921 | 0,49698 | 0,14551 | | | 0,48717 | 0,48125 | 2,07648 | 45,94900 |
| **28H** | 0,40614 | 0,42420 | 0,08481 | | | 0,40398 | 0,41658 | 2,63692 | 52,91144 |
| **28L** | 0,34782 | 0,38714 | 0,10781 | | | 0,34909 | 0,37245 | 6,98874 | 42,01789 |
| **29H** | 0,17024 | 0,13387 | 0,11522 | 0,17168 | 0,24810 | 0,16613 | 0,13155 | 1,70211 | 59,71691 |
| **29L** | 0,13867 | 0,10734 | 0,12774 | 0,03135 | 0,11745 | 0,13880 | 0,10887 | 1,38736 | 60,05318 |
| **30H** | 0,24954 | 0,19539 | 0,17006 | 0,25722 | 0,32430 | 0,23317 | 0,18717 | 1,57851 | 56,18461 |
| **30L** | 0,25627 | 0,18495 | 0,20868 | 0,22000 | 0,29859 | 0,24968 | 0,18186 | 1,36784 | 97,80118 |
| **31H** | 0,29581 | 0,33186 | 0,09279 | 0,20292 | | 0,29193 | 0,33534 | 2,09773 | 40,59673 |
| **31L** | 0,25847 | 0,29439 | 0,09951 | 0,22285 | | 0,26283 | 0,29904 | 2,16905 | 54,61047 |
| **32H** | 0,37795 | 0,46468 | 0,15079 | | | 0,38553 | 0,47491 | 1,81054 | 56,20235 |
| **32L** | 0,34841 | 0,42125 | 0,19925 | | | 0,35335 | 0,45256 | 2,41389 | 52,70371 |
| **33H** | 0,31728 | 0,30717 | 0,04460 | | | 0,31625 | 0,31052 | 2,19967 | 44,20538 |
| **33L** | 0,34796 | 0,34370 | 0,06487 | | | 0,34580 | 0,34550 | 3,64280 | 53,55287 |
| **34H** | 0,23945 | 0,21322 | 0,13052 | | | 0,23650 | 0,21168 | 2,66035 | 51,05320 |
| **34L** | 0,18973 | 0,17477 | 0,09668 | | | 0,19474 | 0,17812 | 1,39245 | 63,79043 |
| **35H** | 0,18363 | 0,17131 | 0,09110 | | | 0,18303 | 0,17251 | 1,92392 | 92,53970 |
| **35L** | 0,19666 | 0,17990 | 0,07664 | | | 0,19579 | 0,18082 | 1,80235 | 77,19243 |
| **36H** | 0,17072 | 0,15934 | 0,11659 | | | 0,17159 | 0,16358 | 1,62006 | 80,66176 |
| **36L** | 0,18631 | 0,17673 | 0,19399 | | | 0,18829 | 0,17670 | 1,42398 | 59,94697 |
| **37H** | 0,31221 | 0,27435 | 0,11569 | | | 0,31364 | 0,27874 | 2,35151 | 39,28045 |
| **37L** | 0,36026 | 0,30563 | 0,11889 | | | 0,35573 | 0,30692 | 2,09398 | 50,13511 |
| **38H** | 0,33681 | 0,33795 | 0,10870 | | | 0,33665 | 0,33931 | 2,22089 | 74,21915 |
| **38L** | 0,33559 | 0,32588 | 0,14758 | | | 0,33634 | 0,33497 | 3,50095 | 51,22044 |

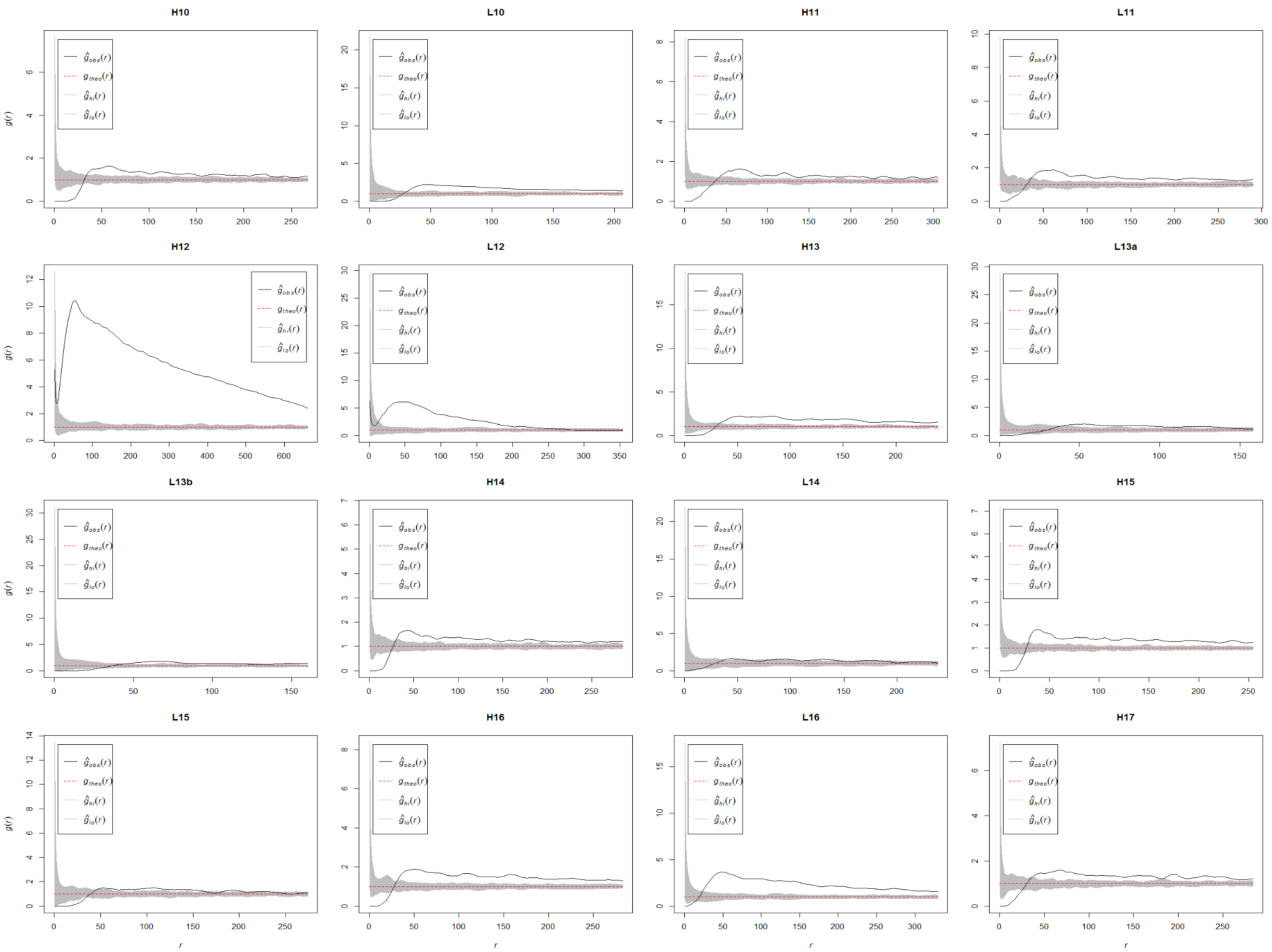
# Appendix B

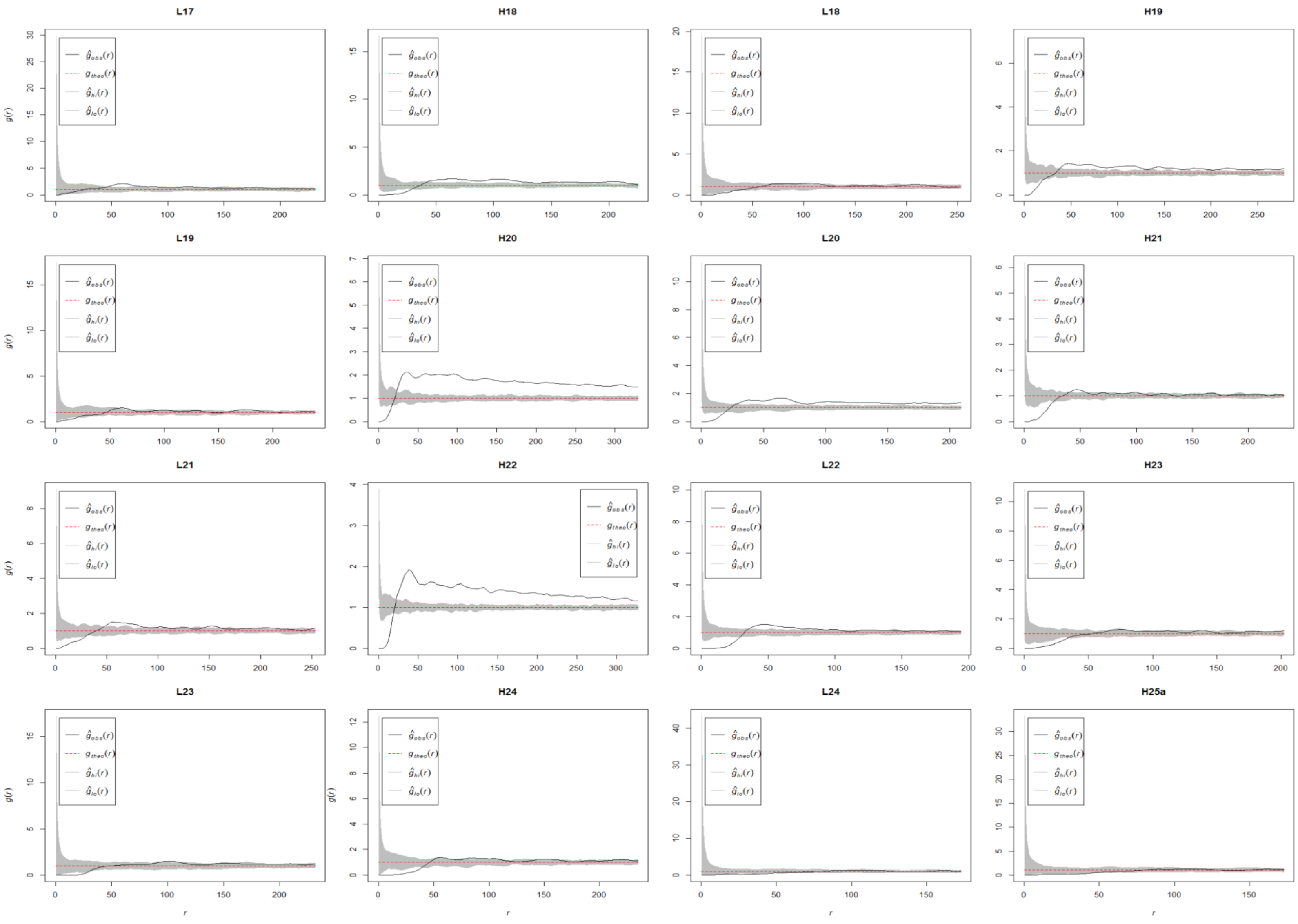
The pair correlation function (PCF) plots for high (H) and low (L) density plots of southern harvest termite (*Microhodotermes viator*) nests across 38 sites, including 95 % simulation envelopes – where g(*r*) extends beyond this envelope the pattern deviates from random dispersion.

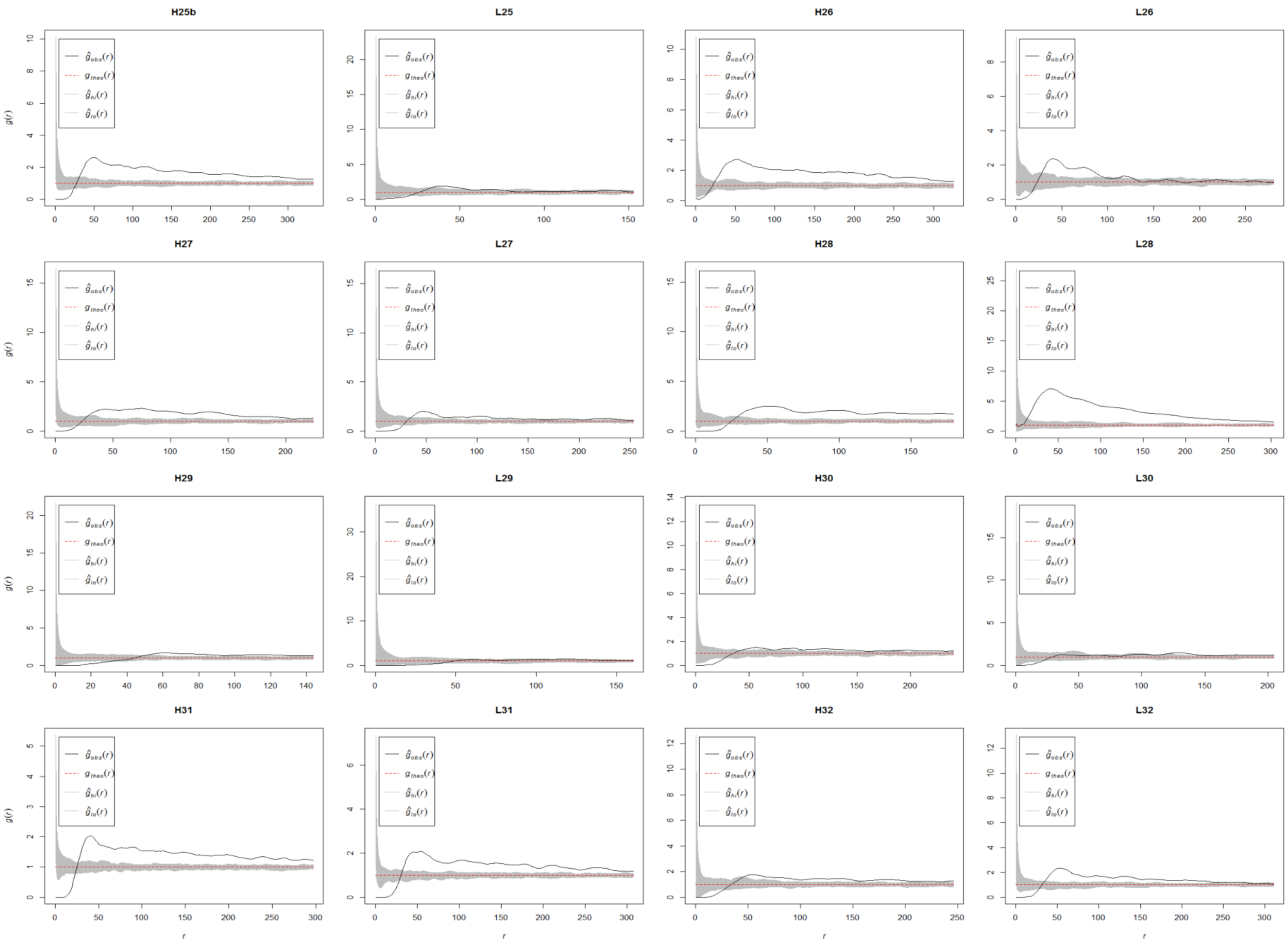


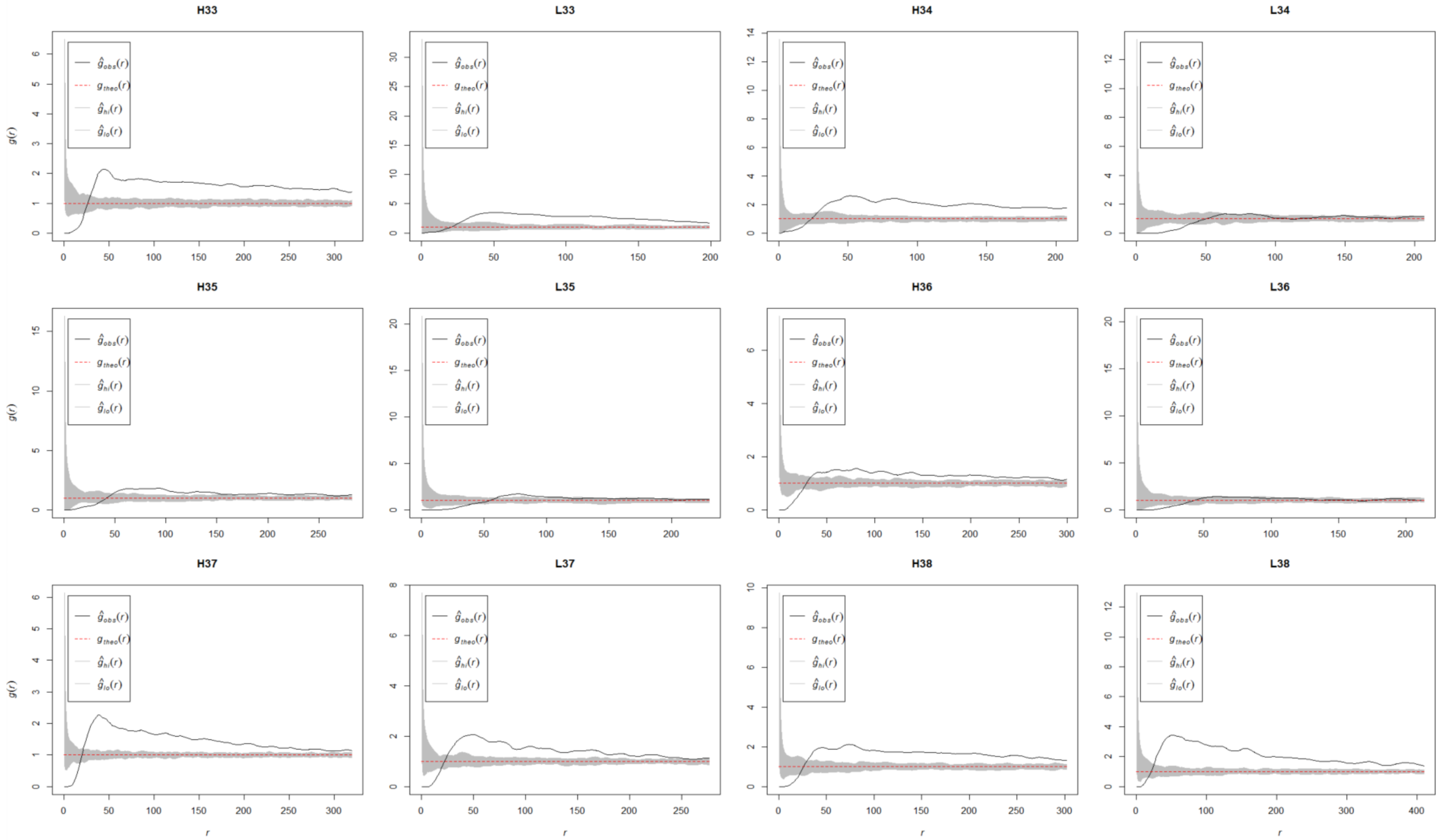



H02
L02
H03
L03
H04
L04
H05
L05
H06
L06
H07
L07
H08
L08
H09
L09
$\hat{g}_{obs}(r)$
$g_{theo}(r)$
$\hat{g}_{hi}(r)$
$\hat{g}_{lo}(r)$
$g(r)$
$r$


H10
L10
H11
L11
H12
L12
H13
L13a
L13b
H14
L14
H15
L15
H16
L16
H17
$g(r)$
$r$
$\hat{g}_{obs}(r)$
$g_{theo}(r)$
$\hat{g}_{hi}(r)$
$\hat{g}_{lo}(r)$


L17
H18
L18
H19
L19
H20
L20
H21
L21
H22
L22
H23
L23
H24
L24
H25a
$\hat{g}_{obs}(r)$
$g_{theo}(r)$
$\hat{g}_{hi}(r)$
$\hat{g}_{lo}(r)$
g(r)
r


H25b
L25
H26
L26
H27
L27
H28
L28
H29
L29
H30
L30
H31
L31
H32
L32
$\hat{g}_{obs}(r)$
$g_{theo}(r)$
$\hat{g}_{hi}(r)$
$\hat{g}_{lo}(r)$
g(r)
r


H33
L33
H34
L34
H35
L35
H36
L36
H37
L37
H38
L38
$\hat{g}_{obs}(r)$
$g_{theo}(r)$
$\hat{g}_{hi}(r)$
$\hat{g}_{lo}(r)$
g(r)
r

# Appendix C

Correlation matrix showing the Pearson's product moment correlation (r) and associated *p*-value ($p < 0.05$ = *; $p < 0.01$ = **; $p < 0.001$ = ***) between variables; density (high = red, low = blue), nearest neighbour distance (NN), R-dispersion coefficient (Rcoef), percentage hexagons in Voronoi tessellation (Hex), *Microhodotermes viator* nest diameter, mean annual precipitation (MAP), autumn (A) and spring (S) productivity (NDVI), and biome according to Mucina and Rutherford (2006).

| | | Density | NN | Rcoef | Hex | Diameter | MAP | NDVI-A | NDVI-S | Biome |
|---|---|---|---|---|---|---|---|---|---|---|
| **Density** | r | 1,0000 | -0,8318 | 0,1215 | 0,4306 | 0,1737 | -0,2820 | 0,1409 | 0,0652 | 0,0263 |
| | *p*-value | NA | 0,0000*** | 0,4673 | 0,007** | 0,2971 | 0,0863 | 0,3990 | 0,6973 | 0,8757 |
| **NN** | r | -0,7443 | 1,0000 | -0,2183 | -0,3623 | -0,0752 | 0,2144 | -0,2187 | -0,1825 | -0,1254 |
| | *p*-value | 0,0000*** | NA | 0,1879 | 0,0254* | 0,6537 | 0,1962 | 0,1871 | 0,2728 | 0,4531 |
| **Rcoef** | r | 0,1390 | 0,3399 | 1,0000 | 0,1917 | 0,2119 | -0,5152 | -0,3411 | -0,2834 | 0,4973 |
| | *p*-value | 0,4052 | 0,0368* | NA | 0,2488 | 0,2016 | 0,0009*** | 0,0361* | 0,0846 | 0,0015** |
| **Hex** | r | 0,3646 | -0,2256 | 0,0714 | 1,0000 | 0,0943 | 0,0114 | 0,0923 | 0,0662 | 0,0116 |
| | *p*-value | 0,0244* | 0,1732 | 0,6702 | NA | 0,5732 | 0,9456 | 0,5816 | 0,6927 | 0,9450 |
| **Diameter** | r | 0,0809 | -0,0989 | 0,1540 | 0,0897 | 1,0000 | -0,2362 | 0,0895 | 0,1553 | 0,2011 |
| | *p*-value | 0,6291 | 0,5546 | 0,3557 | 0,5922 | NA | 0,1534 | 0,5932 | 0,3519 | 0,2260 |
| **MAP** | r | -0,2186 | -0,1535 | -0,5099 | -0,1156 | -0,0966 | 1,0000 | 0,3914 | 0,3907 | -0,3993 |
| | *p*-value | 0,1874 | 0,3575 | 0,0011** | 0,4897 | 0,5640 | NA | 0,0151* | 0,0153* | 0,013* |
| **NDVI-A** | r | 0,1573 | -0,4787 | -0,5242 | 0,0679 | 0,0496 | 0,4171 | 1,0000 | 0,9669 | -0,5490 |
| | *p*-value | 0,3456 | 0,0024** | 0,0007*** | 0,6855 | 0,7673 | 0,0092** | NA | 0,0000*** | 0,0004*** |
| **NDVI-S** | r | 0,1133 | -0,4679 | -0,5765 | 0,0950 | 0,1584 | 0,4426 | 0,9479 | 1,0000 | -0,4720 |
| | *p*-value | 0,4984 | 0,0031** | 0,0002*** | 0,5705 | 0,3421 | 0,0054** | 0,0000*** | NA | 0,0028** |
| **Biome** | r | -0,0120 | 0,2325 | 0,1711 | -0,0545 | 0,2093 | -0,3651 | -0,6145 | -0,5085 | 1,0000 |
| | *p*-value | 0,9432 | 0,1600 | 0,3045 | 0,7451 | 0,2073 | 0,0242* | 0,0000*** | 0,0011** | NA |

# Appendix D

Numeric values (code) given to each biome, bioregion and vegetation unit assigned to plots used in this study according to Mucina and Rutherford (2006).

| Biome | Code | Vegetation unit | Code |
|---|---|---|---|
| Albany Thicket | 1 | Great bush thicket (AT11) | 7 |
| Fynbos | 2 | Groot thicket/Southern karoo riviere (AT3/AZi6) | 8 |
| Succulent Karoo | 3 | Knersvlakte shale vygieveld (SKk4) | 9 |
| **Bioregion** | **Code** | Knysna sand fynbos (FFd10) | 10 |
| NA | 0 | Koedoesberge moordenaars karoo/Matjiesfontein shale renosterveld (SKv6/FRs6) | 11 |
| Granite Fynbos/Sandstone Fynbos/Shale Fynbos | 1 | Little karoo quartz vygieveld (SKv10) | 12 |
| Inland Saline Vegetation | 2 | Matjiesfontein shale renosterveld (FRs6) | 13 |
| Knersvlakte | 3 | Montagu shale renosterveld (FRs7) | 14 |
| Namaqualand Hardeveld | 4 | Montagu shale renosterveld/Western little karoo (FRs7/SKv8) | 15 |
| Sand Fynbos | 6 | Namaqualand klipkoppe shrubland (SKn1) | 16 |
| Sandstone Fynbos | 7 | Namaqualand standveld/Namaqualand heulwetjieveld (SKs7/SKn4) | 17 |
| Shale Fynbos/Shale Renosterveld | 8 | Prince Albert succulent karoo (SKv13) | 18 |
| Shale Renosterveld | 9 | Robertson karoo/Matjiesfontein shale renosterveld (SKv7/FRs6) | 19 |
| **Vegetation unit** | **Code** | Southern karoo riviere (AZi6) | 20 |
| Agter Sederberg shrubland (SKv3 ) | 1 | Swartland shale renosterveld (FRs9) | 21 |
| Boland granite fynbos/Bokkeveld sandstone fynbos/Cape winelands shale fynbos (FFg2/FFs1/FFh5) | 2 | Tanqua karoo (SKv5) | 22 |
| Breede shale fynbos/Breede shale renosterveld (FFh4/FRs8) | 3 | Vanrhynsdorp gannabosveld/Knersvlakte dolomite vygieveld (SKk5/SKk6) | 23 |
| Citrusdal vygieveld (SKk7) | 4 | Western little karoo (SKv8 ) | 24 |
| Eastern little karoo (SKv11) | 5 | Winterhoek sandstone fynbos (FFs5) | 25 |
| Gamka thicket (AT2) | 6 | | |

# Appendix E

The *p*-values of variables; intercept, nearest neighbour distance, R-dispersion coefficient, percentage hexagons, *Microhodotermes viator* nest diameter, mean annual precipitation, autumn and spring productivity (NDVI), biome, bioregion and vegetation unit (Mucina and Rutherford, 2006) for models explored in Chapter 2 predicting *M. viator* nest density and dispersion respectively.

| | **OMA1, $p < 0{,}001$, $R^2$ = 0,70** | **OMS1, $p < 0{,}001$, $R^2$ = 0,70** | **OM-NDVI, $p < 0{,}001$, $R^2$ = 69** | **OMA-MAP, $p < 0{,}001$, R2 = 0,68** | **OMS-MAP, $p < 0{,}001$, $R^2$ = 0,69** |
|---|---|---|---|---|---|
| **intercept** | 0,0002 | 0,0000 | 0,0000 | 0,0006 | 0,0000 |
| **nn** | 0,0000 | 0,0000 | 0,0000 | 0,0000 | 0,0000 |
| **rcoef** | 0,5087 | 0,6820 | 0,3420 | 0,1886 | 0,3513 |
| **hex** | 0,0422 | 0,0360 | 0,0430 | 0,0533 | 0,0436 |
| **diameter** | 0,6702 | 0,4720 | 0,8080 | 0,6466 | 0,4276 |
| **map** | 0,1478 | 0,1870 | 0,1290 | - | - |
| **modis_a** | 0,5013 | - | - | 0,4271 | - |
| **modis_s** | - | 0,2050 | - | - | 0,1417 |
| **biome** | 0,9011 | 0,7480 | 0,7960 | 0,8154 | 0,9902 |
| **bioregion** | 0,1998 | 0,3030 | 0,1590 | 0,0986 | 0,1884 |
| **veg unit** | 0,8571 | 0,7960 | 0,9290 | 0,7643 | 0,7048 |

| | **SKMA1, $p < 0{,}001$, $R^2$ = 0,78** | **SKMS1, $p < 0{,}001$, $R^2$ = 0,78** | **SKM-NDVI, $p < 0{,}001$, $R^2$ = 0,77** | **SKMA-MAP, $p < 0{,}001$, $R^2$ = 0,78** | **SKMS-MAP, $p < 0{,}001$, $R^2$ = 0,78** |
|---|---|---|---|---|---|
| **intercept** | 0,0011 | 0,0005 | 0,0001 | 0,0010 | 0,0005 |
| **nn** | 0,0000 | 0,0000 | 0,0000 | 0,0000 | 0,0000 |
| **rcoef** | 0,0451 | 0,0806 | 0,1267 | 0,0353 | 0,0655 |
| **hex** | 0,4646 | 0,3947 | 0,1578 | 0,4736 | 0,4030 |
| **diameter** | 0,3314 | 0,4209 | 0,7414 | 0,3205 | 0,4097 |
| **map** | 0,7650 | 0,7331 | 0,6932 | - | - |
| **modis_a** | 0,1881 | - | - | 0,1754 | - |

| | **SKMA1, $p$ < 0,001, $R^2$ = 0,78** | **SKMS1, $p$ < 0,001, $R^2$ = 0,78** | **SKM-NDVI, $p$ < 0,001, $R^2$ = 0,77** | **SKMA-MAP, $p$ < 0,001, $R^2$ = 0,78** | **SKMS-MAP, $p$ < 0,001, $R^2$ = 0,78** |
|---|---|---|---|---|---|
| **modis_s** | - | 0,3557 | - | - | 0,3404 |
| **bioregion** | 0,4983 | 0,6821 | 0,8612 | 0,3873 | 0,5536 |
| **veg unit** | 0,7637 | 0,8161 | 0,7971 | 0,6779 | 0,7226 |

| | **OSA1, $p$ < 0,001, $R^2$ = 0,70** | **OSA1-MAP, $p$ < 0,001, $R^2$ = 0,69** | **SKSA1, $p$ < 0,001, $R^2$ = 0,79** | **SKSA1-MAP, $p$ < 0,001, $R^2$ = 0,79** | **OSA1-NDVI, $p$ < 0,001, $R^2$ = 69** | **SKSA1-NDVI, $p$ < 0,001, $R^2$ = 0,77** |
|---|---|---|---|---|---|---|
| **intercept** | 0,0000 | 0,0001 | 0,0000 | 0,0000 | 0,0000 | 0,0001 |
| **nn** | 0,0000 | 0,0000 | 0,0000 | 0,0000 | 0,0000 | 0,0000 |
| **rcoef** | 0,2892 | 0,0499 | 0,0870 | 0,0698 | 0,3420 | 0,1267 |
| **hex** | 0,0354 | 0,0498 | 0,1150 | 0,1152 | 0,0430 | 0,1578 |
| **diameter** | 0,7219 | 0,7949 | 0,3690 | 0,3629 | 0,8080 | 0,7414 |
| **map** | 0,0830 | - | 0,7100 | - | 0,1290 | 0,6932 |
| **spot_old** | 0,1191 | 0,1906 | 0,1260 | 0,1211 | - | - |
| **biome** | 0,7958 | 0,6955 | - | - | - | - |
| **bioregion** | 0,0988 | 0,0401 | 0,7340 | 0,5972 | 0,7960 | 0,8612 |
| **veg unit** | 0,8818 | 0,7937 | 0,8180 | 0,7163 | 0,1590 | 0,7971 |

| | **OSA2, $p$ < 0,001, $R^2$ = 0,79** | **OSA2-MAP, $p$ < 0,001, $R^2$ = 0,76** | **SKSA2, $p$ < 0,001, $R^2$ = 0,80** | **SKSA2 - MAP, $p$ < 0,001, $R^2$ = 0,78** | **OSA2-NDVI, $p$ < 0,001, $R^2$ = 0,71** | **SKSA2-NDVI, $p$ < 0,01, $R^2$ = 0,77** |
|---|---|---|---|---|---|---|
| **intercept** | 0,0010 | 0,0054 | 0,0041 | 0,0066 | 0,0137 | 0,0101 |
| **nn** | 0,0000 | 0,0000 | 0,0000 | 0,0000 | 0,0000 | 0,0001 |
| **rcoef** | 0,1741 | 0,6465 | 0,8906 | 0,7115 | 0,2433 | 0,6317 |
| **hex** | 0,0586 | 0,0791 | 0,2228 | 0,3218 | 0,0601 | 0,248 |
| **diameter** | 0,2843 | 0,3096 | 0,8946 | 0,9174 | 0,6573 | 0,4473 |
| **map** | 0,0553 | - | 0,2650 | - | 0,4340 | 0,5575 |
| **spot_new_a** | 0,0054 | 0,0278 | 0,1160 | 0,2006 | - | - |

| | **OSA2, $p$ < 0,001, $R^2$ = 0,79** | **OSA2-MAP, $p$ < 0,001, $R^2$ = 0,76** | **SKSA2, $p$ < 0,001, $R^2$ = 0,80** | **SKSA2 - MAP, $p$ < 0,001, $R^2$ = 0,78** | **OSA2-NDVI, $p$ < 0,001, $R^2$ = 0,71** | **SKSA2-NDVI, $p$ < 0,01, $R^2$ = 0,77** |
|---|---|---|---|---|---|---|
| **biome** | 0,2638 | 0,1606 | - | - | 0,5515 | - |
| **bioregion** | 0,0394 | 0,0895 | 0,0622 | 0,0807 | 0,9752 | 0,2843 |
| **veg unit** | 0,3515 | 0,3977 | 0,4899 | 0,4471 | 0,3215 | 0,5005 |

| | **OSS1, $p$ < 0,001, $R^2$ = 0,76** | **OSS1-MAP, $p$ < 0,001, $R^2$ = 0,73** | **SKSS1, $p$ < 0,001, $R^2$ = 0,76** | **SKS1-MAP, $p$ < 0,001, $R^2$ = 0,75** | **OSS1-NDVI, $p$ < 0,001, $R^2$ = 0,71** | **SKSS1-NDVI, $p$ < 0,01, $R^2$ = 0,77** |
|---|---|---|---|---|---|---|
| **intercept** | 0,0078 | 0,0247 | 0,0212 | 0,0232 | 0,0137 | 0,0101 |
| **nn** | 0,0000 | 0,0000 | 0,0002 | 0,0000 | 0,0000 | 0,0001 |
| **rcoef** | 0,2989 | 0,7171 | 0,8784 | 0,7060 | 0,2433 | 0,6317 |
| **hex** | 0,0466 | 0,0470 | 0,1791 | 0,2193 | 0,0601 | 0,248 |
| **diameter** | 0,1661 | 0,2599 | 0,8105 | 0,7033 | 0,6573 | 0,4473 |
| **map** | 0,1223 | - | 0,4864 | - | 0,4340 | 0,5575 |
| **spot_new_s** | 0,0325 | 0,0782 | 0,8085 | 0,9981 | - | - |
| **biome** | 0,7987 | 0,5828 | - | `- | 0,5515 | - |
| **bioregion** | 0,4802 | 0,3630 | 0,5042 | 0,4123 | 0,9752 | 0,2843 |
| **veg unit** | 0,3485 | 0,5188 | 0,4656 | 0,5104 | 0,3215 | 0,5005 |

# Appendix F

The mean annual rainfall of each site and their associated carbon, calcium and nitrogen concentrations for both habitat treatments (*Mirohodotermes viator* nests and matrix soils).

| **Site** | **Rainfall (mm)** | **Matrix** | | | ***M. viator* nest** | | |
|---|---|---|---|---|---|---|---|
| | | **Carbon (%)** | **Calcium (cmol/kg)** | **Nitrogen (%)** | **Carbon (%)** | **Calcium (cmol/kg)** | **Nitrogen (%)** |
| **Prince Albert** | 144,45 | 2,044 | 3,961 | 0,15 | 2,237 | 2,199 | 0,1238 |
| **Vanrhynsdorp** | 162,88 | 2,154 | 12,47 | 0,1954 | 4,065 | 25,319 | 0,3369 |
| **Clanwilliam** | 182,2 | 0,516 | 0,625 | 0,0269 | 0,686 | 2,863 | 0,0614 |
| **Oudtshoorn** | 244,73 | 3,975 | 9,499 | 0,2876 | 3,801 | 9,35 | 0,3186 |
| **Calitzdorp** | 244,73 | 1,518 | 1,064 | 0,0916 | 3,681 | 4,101 | 0,2498 |
| **Worcester** | 285,78 | 1,914 | 15,984 | 0,1866 | 3,978 | 36,354 | 0,3235 |
| **Malmesbury** | 348,63 | 1,428 | 13,225 | 0,1408 | 3,779 | 19,559 | 0,2432 |
| **Koringberg** | 359,1 | 4,278 | 6,999 | 0,2306 | 4,656 | 12,47 | 0,3339 |
| **Tulbagh** | 777,65 | 2,29 | 4,195 | 0,1469 | 2,537 | 5,222 | 0,17 |
| **Stellenbosch** | 1060,14 | 0,403 | 1,887 | 0,0468 | 0,977 | 13,607 | 0,0948 |

# Appendix G

Watering schedule for germination trials at the Plant Propagation Unit, W.H Pearson Building, University of Cape Town.

| Date | ml | Date | ml | Date | ml |
|---|---|---|---|---|---|
| 25 May 2017 | 150 | 27 June 2017 | 150 | 11 August 2017 | 250 |
| 26 May 2017 | 150 | 28 June 2017 | 150 | 17 August 2017 | 250 |
| 27 May 2017 | 150 | 29 June 2017 | 150 | 26 August 2017 | 250 |
| 28 May 2017 | 150 | 30 June 2017 | 150 | 28 August 2017 | 250 |
| 29 May 2017 | 150 | 01 July 2017 | 150 | 04 September 2017 | 250 |
| 30 May 2017 | 150 | 02 July 2017 | 150 | 07 September 2017 | 250 |
| 31 May 2017 | 150 | 03 July 2017 | 150 | 08 September 2017 | 250 |
| 01 June 2017 | 150 | 04 July 2017 | 150 | 10 September 2017 | 250 |
| 02 June 2017 | 150 | 05 July 2017 | 150 | 12 September 2017 | 250 |
| 03 June 2017 | 150 | 06 July 2017 | 150 | 14 September 2017 | 250 |
| 04 June 2017 | 150 | 07 July 2017 | 150 | 17 September 2017 | 250 |
| 05 June 2017 | 150 | 08 July 2017 | 150 | 20 September 2017 | 250 |
| 06 June 2017 | 150 | 09 July 2017 | 150 | 22 September 2017 | 250 |
| 07 June 2017 | 150 | 10 July 2017 | 150 | 24 September 2017 | 250 |
| 08 June 2017 | 150 | 11 July 2017 | 150 | 26 September 2017 | 250 |
| 09 June 2017 | 150 | 12 July 2017 | 150 | 28 September 2017 | 250 |
| 10 June 2017 | 150 | 13 July 2017 | 150 | 30 September 2017 | 250 |
| 11 June 2017 | 150 | 14 July 2017 | 150 | 02 October 2017 | 250 |
| 12 June 2017 | 150 | 15 July 2017 | 150 | 04 October 2017 | 250 |
| 13 June 2017 | 150 | 16 July 2017 | 150 | 06 October 2017 | 250 |
| 14 June 2017 | 150 | 17 July 2017 | 150 | 07 October 2017 | 250 |
| 15 June 2017 | 150 | 18 July 2017 | 150 | 09 October 2017 | 250 |
| 16 June 2017 | 150 | 19 July 2017 | 150 | 11 October 2017 | 250 |
| 17 June 2017 | 150 | 20 July 2017 | 150 | 14 October 2017 | 250 |
| 18 June 2017 | 150 | 21 July 2017 | 150 | 16 October 2017 | 250 |
| 19 June 2017 | 150 | 22 July 2017 | 150 | 18 October 2017 | 250 |
| 20 June 2017 | 150 | 23 July 2017 | 150 | 21 October 2017 | 250 |
| 21 June 2017 | 150 | 24 July 2017 | 150 | 23 October 2017 | 250 |
| 22 June 2017 | 150 | 25 July 2017 | 150 | 25 October 2017 | 250 |
| 23 June 2017 | 150 | 26 July 2017 | 150 | 27 October 2017 | 250 |
| 24 June 2017 | 150 | 27 July 2017 | 150 | 31 October 2017 | 250 |
| 25 June 2017 | 150 | 28 July 2017 | 150 | | |
| 26 June 2017 | 150 | 03 August 2017 | 250 | | |

# Appendix H

Summary of multiple linear regression models used to predict dependent growth variables (difference in root and shoot length, and number of leaves/branches) of *Aloe microstigma*, *Pteronia incana*, *P. paniculata*, and *Tylecodon paniculatus* in response to independent variables (carbon, calcium and nitrogen concentration, and mean soil particle size, water holding capacity, water percolation rate and water retention time) and reduced data variables *NutrientsPC*, *SoilPC1* and *SoilPC2* ( . = p < 0.1; * = p < 0,05; ** = p < 0,01; *** = p < 0,001).

| ***Aloe microstigma* root growth** | **Model 1 (*p* = 0,03)** | **Model 2 (*p* = 0,93)** | **Model 3 (*p* = 0,18)** |
|---|---|---|---|
| Intercept | 0,85084 | 0,0978 **.** | 0,5972 |
| Habitat | 0,01642* | 0,6375 | 0,1162 |
| Carbon | 0,509 | | |
| Calcium | 0,00212** | | 0,0771 **.** |
| Nitrogen | 0,44389 | | |
| Mean soil particle size | 0,04657* | | 0,4424 |
| Water holding capacity | 0,43254 | | |
| Percolation rate | 0,00425** | | 0,0931 **.** |
| Retention time | 0,13764 | | |
| *NutrientsPC* | | 0,9594 | |
| *SoilPC1* | | 0,583 | |
| *SoilPC2* | | 0,6328 | |

| ***Aloe microstigma* shoot growth** | **Model 1 (*p* = 0,65)** | **Model 2 (*p* = 0,36)** | **Model 3 (*p* = 0,58)** |
|---|---|---|---|
| Intercept | 0,818 | 0,00371** | 0,0105* |
| Habitat | 0,372 | 0,1808 | 0,479 |
| Carbon | 0,686 | | |
| Calcium | 0,57 | | |
| Nitrogen | 0,229 | | |
| Mean soil particle size | 0,531 | | |
| Water holding capacity | 0,747 | | |
| Percolation rate | 0,76 | | |
| Retention time | 0,22 | | |
| *NutrientsPC* | | 0,09483 **.** | 0,3169 |
| *SoilPC1* | | 0,2181 | |
| *SoilPC2* | | 0,25202 | |

| ***Aloe microstigma* leaf growth** | **Model 1 (*p* = 0,22)** | **Model 2 (*p* = 0,05)** | **Model 3 (*p* = 0,03)** |
|---|---|---|---|
| Intercept | 0,4724 | 0,97 | 0,9393 |
| Habitat | 0,0182* | 0,0294* | 0,0312* |
| Carbon | 0,9297 | | |
| Calcium | 0,2157 | | |
| Nitrogen | 0,4204 | | |

| | | | |
|---|---|---|---|
| Mean soil particle size | 0,4757 | | |
| Water holding capacity | 0,2636 | | |
| Percolation rate | 0,1145 | | |
| Retention time | 0,8473 | | |
| *NutrientsPC* | | 0,0206* | 0,0101* |
| *SoilPC1* | | 0,4317 | |
| *SoilPC2* | | 0,0835 **.** | 0,0624 **.** |

| ***Aloe microstigma* health** | **Model 1 (*p* = 0,32)** | **Model 2 (*p* = 0,23)** |
|---|---|---|
| Intercept | 0,0429* | 0,000000427*** |
| Habitat | 0,679 | 0,0294* |
| Carbon | 0,6777 | |
| Calcium | 0,2773 | |
| Nitrogen | 0,6412 | |
| Mean soil particle size | 0,9358 | |
| Water holding capacity | 0,2724 | |
| Percolation rate | 0,1204 | |
| Retention time | 0,4068 | |
| *NutrientsPC* | | 0,0206* |
| *SoilPC1* | | 0,4317 |
| *SoilPC2* | | 0,0835 **.** |

| ***Pteronia incana* root growth** | **Model 1 (*p* = 0,41)** | **Model 2 (*p* = 0,26)** | **Model 3 (*p* = 0,10)** |
|---|---|---|---|
| Intercept | 0,891 | 0,0218* | 0,00715** |
| Habitat | 0,297 | 0,4752 | 0,28404 |
| Carbon | 0,258 | | |
| Calcium | 0,401 | | |
| Nitrogen | 0,84 | | |
| Mean soil particle size | 0,473 | | |
| Water holding capacity | 0,142 | | |
| Percolation rate | 0,494 | | |
| Retention time | 0,907 | | |
| *NutrientsPC* | | 0,0563 , | 0,03252 , |
| *SoilPC1* | | 0,4714 | |
| *SoilPC2* | | 0,5373 | |

| ***Pteronia incana* shoot growth** | **Model 1 (*p* = 0,42)** | **Model 2 (*p* = 0,28)** | **Model 3 (*p* = 0,09)** | **Model 4 (*p* = 0,16)** | **Model 5 (p = 0,42)** |
|---|---|---|---|---|---|
| Intercept | 0,5514 | 0,00495** | 0,23828 | 0,00176** | -4,121 |
| Habitat | 0,4675 | 0,9204 | 0,4925 | 0,81832 | -10,002 |
| Carbon | 0,4301 | | | | |
| Calcium | 0,9536 | | | | |
| Nitrogen | 0,082 | | 0,0182* | | |
| Mean soil particle size | 0,7757 | | | | |
| Water holding capacity | 0,0679 | | 0,0161* | | |
| Percolation rate | 0,6992 | | | | |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Retention time | 0,3581 |  |  |  | -2,069 |
| *NutrientsPC* |  | 0,05834 |  | 0,05517 , |  |
| *SoilPC1* |  | 0,03367* |  | 0,03157* |  |
| *SoilPC2* |  | 0,83188 |  |  |  |
| ***Pteronia incana* branch growth** | **Model 1 (*p* = 0,80)** | **Model 2 (*p* = 0,48)** |  |  |  |
| Intercept | 0,944 | 0,482 |  |  |  |
| Habitat | 0,623 | 0,891 |  |  |  |
| Carbon | 0,6 |  |  |  |  |
| Calcium | 0,3 |  |  |  |  |
| Nitrogen | 0,51 |  |  |  |  |
| Mean soil particle size | 0,747 |  |  |  |  |
| Water holding capacity | 0,704 |  |  |  |  |
| Percolation rate | 0,721 |  |  |  |  |
| Retention time | 0,61 |  |  |  |  |
| *NutrientsPC* |  | 0,103 |  |  |  |
| *SoilPC1* |  | 0,343 |  |  |  |
| *SoilPC2* |  | 0,989 |  |  |  |
| ***Pteronia incana* health** | **Model 1 (*p* = 0,71)** | **Model 2 (*p* = 0,51)** |  |  |  |
| Intercept | 0,235 | 0,000000447*** |  |  |  |
| Habitat | 0,886 | 0,449 |  |  |  |
| Carbon | 0,144 |  |  |  |  |
| Calcium | 0,524 |  |  |  |  |
| Nitrogen | 0,226 |  |  |  |  |
| Mean soil particle size | 0,646 |  |  |  |  |
| Water holding capacity | 0,788 |  |  |  |  |
| Percolation rate | 0,444 |  |  |  |  |
| Retention time | 0,882 |  |  |  |  |
| *NutrientsPC* |  | 0,215 |  |  |  |
| *SoilPC1* |  | 0,856 |  |  |  |
| *SoilPC2* |  | 0,597 |  |  |  |
| ***Pteronia paniculata* root growth** | **Model 1 (*p* = 0,41)** | **Model 2 (*p* = 0,16)** | **Model 3 (*p* = 0,05)** | **Model 4 (*p* = 0,11)** |  |
| Intercept | 0,8309 | 0,1103 | 0,00659** | 0,1567 |  |
| Habitat | 0,7998 | 0,7443 | 0,65918 | 0,9559 |  |
| Carbon | 0,6403 |  |  |  |  |
| Calcium | 0,5653 |  |  |  |  |
| Nitrogen | 0,7662 |  |  |  |  |
| Mean soil particle size | 0,8995 |  |  |  |  |
| Water holding capacity | 0,6842 |  |  |  |  |
| Percolation rate | 0,0416* |  | 0,02313* |  |  |
| Retention time | 0,4201 |  |  |  |  |
| *NutrientsPC* |  | 0,1637 |  |  |  |
| *SoilPC1* |  | 0,1775 |  |  |  |

| | | | | |
|---|---|---|---|---|
| *SoilPC2* | | 0,0506 | | 0,0626 |

| ***Pteronia paniculata* shoot growth** | **Model 1 (*p* = 0,18)** | **Model 2 (*p* = 0,09)** | **Model 3 (*p* = 0,48)** | **Model 4 (p = 0,07)** |
|---|---|---|---|---|
| Intercept | 0,1726 | 0,000000281*** | 0,162 | 0,0000976*** |
| Habitat | 0,0874 | 0,0197* | 0,263 | 0,0566 . |
| Carbon | 0,2921 | | | |
| Calcium | 0,1451 | | | |
| Nitrogen | 0,289 | | | 0,0399* |
| Mean soil particle size | 0,0863 | | 0,492 | |
| Water holding capacity | 0,5335 | | | |
| Percolation rate | 0,9555 | | | |
| Retention time | 0,5665 | | | |
| *NutrientsPC* | | 0,1295 | | |
| *SoilPC1* | | 0,7738 | | |
| *SoilPC2* | | 0,2296 | | |

| ***Pteronia paniculata* branch growth** | **Model 1 (*p* = 0,74)** | **Model 2 (*p* = 0,42)** | **Model 3 (*p* = 0,23)** |
|---|---|---|---|
| Intercept | 0,842 | 0,7917 | 0,472 |
| Habitat | 0,503 | 0,108 | 0,182 |
| Carbon | 0,798 | | |
| Calcium | 0,931 | | |
| Nitrogen | 0,704 | | |
| Mean soil particle size | 0,214 | | |
| Water holding capacity | 0,243 | | |
| Percolation rate | 0,916 | | |
| Retention time | 0,473 | | |
| *NutrientsPC* | | 0,5218 | |
| *SoilPC1* | | 0,9564 | |
| *SoilPC2* | | 0,0966 | 0,109 |

| ***Pteronia paniculata* health** | **Model 1 (*p* = 0,10)** | **Model 2 (*p* = 0,01)** | **Model 3 (*p* = 0,001)** |
|---|---|---|---|
| Intercept | 0,03197* | 8,49 x 10-16 | 2 x 10-16 |
| Habitat | 0,00677** | 0,00154** | 0,000416*** |
| Carbon | 0,53519 | | |
| Calcium | 0,75742 | | |
| Nitrogen | 0,63642 | | |
| Mean soil particle size | 0,43745 | | |
| Water holding capacity | 0,8893 | | |
| Percolation rate | 0,03268* | | 0,004883** |
| Retention time | 0,6707 | | |
| *NutrientsPC* | | 0,97249 | |
| *SoilPC1* | | 0,48306 | |
| *SoilPC2* | | 0,00882** | |

| ***Tylecodon paniculatus* root growth** | **Model 1 (*p* = 0,56)** | **Model 2 (*p* = 0,54)** | **Model 3 (p = 0,10)** |
|---|---|---|---|
| Intercept | 0,529 | 0,040* | 0,5099 |

|  |  |  |  |  |
|---|---|---|---|---|
| Habitat | 0,688 | 0,478 | 0,2875 |  |
| Carbon | 0,336 |  |  |  |
| Calcium | 0,299 |  |  |  |
| Nitrogen | 0,103 |  | 0,0328* |  |
| Mean soil particle size | 0,924 |  |  |  |
| Water holding capacity | 0,971 |  |  |  |
| Percolation rate | 0,543 |  |  |  |
| Retention time | 0,868 |  |  |  |
| *NutrientsPC* |  | 0,281 |  |  |
| *SoilPC1* |  | 0,914 |  |  |
| *SoilPC2* |  | 0,913 |  |  |
| ***Tylecodon paniculatus* shoot growth** | **Model 1 (*p* = 0,68)** | **Model 2 (*p* = 0,95)** | **Model 3 (*p* = 0,64)** |  |
| Intercept | 0,8201 | 0,00294** | 0,0063** |  |
| Habitat | 0,622 | 0,66135 | 0,8921 |  |
| Carbon | 0,515 |  |  |  |
| Calcium | 0,117 |  | 0,4773 |  |
| Nitrogen | 0,348 |  |  |  |
| Mean soil particle size | 0,369 |  |  |  |
| Water holding capacity | 0,412 |  |  |  |
| Percolation rate | 0,164 |  |  |  |
| Retention time | 0,241 |  |  |  |
| *NutrientsPC* |  | 0,86067 |  |  |
| *SoilPC1* |  | 0,62862 |  |  |
| *SoilPC2* |  | 0,88299 |  |  |
| ***Tylecodon paniculatus* leaf growth** | **Model 1 (*p* = 0,04)** | **Model 2 (*p* = 0,66)** | **Model 3 (*p* = 0,48)** | **Model 4 (p = 0,4)** |
| Intercept | 0,95588 | 0,216 | 0,0147* | 0,6061 |
| Habitat | 0,16359 | 0,778 | 0,4949 | 0,7891 |
| Carbon | 0,48072 |  |  | 0,1908 |
| Calcium | 0,00795** |  | 0,7953 | 0,0648 . |
| Nitrogen | 0,14494 |  |  | 0,0899 . |
| Mean soil particle size | 0,04471* |  | 0,1356 |  |
| Water holding capacity | 0,1522 |  |  | 0,8852 |
| Percolation rate | 0,03889* |  | 0,4221 |  |
| Retention time | 0,01253* |  | 0,3428 |  |
| *NutrientsPC* |  | 0,398 |  |  |
| *SoilPC1* |  | 0,28 |  |  |
| *SoilPC2* |  | 0,357 |  |  |
| ***Tylecodon paniculatus* health** | **Model 1 (*p* = 0,34)** | **Model 2 (*p* = 0,65)** | **Model 3 (*p* = 0,16)** |  |
| Intercept | 0,2479 | 0,00000759*** | 0,0000996*** |  |
| Habitat | 0,8334 | 0,401 | 0,4996 |  |
| Carbon | 0,4758 |  |  |  |
| Calcium | 0,1588 |  |  |  |
| Nitrogen | 0,2438 |  |  |  |

| | | | |
|---|---|---|---|
| Mean soil particle size | 0,0618 | | 0,0596 |
| Water holding capacity | 0,4341 | | |
| Percolation rate | 0,1819 | | |
| Retention time | 0,1379 | | |
| *NutrientsPC* | | 0,38 | |
| *SoilPC1* | | 0,32 | |
| *SoilPC2* | | 0,294 | |

# Appendix I

The raw data table of germination and survival of seeds for three species associated exclusively with *Microhodotermes viator* nest habitats (*Aloe microstigma*, *Pteronia incana*, and *Tylecodon paniculatus*), and three species associated exclusively with matrix habitats (*Anginon* sp., *Pteronia paniculata*, and *Ruschia decurvans*) in reciprocal soil treatments from both habitats.

| **Pot number:** | **Soil treatment:** | **Species:** | **Total germinated:** | **Survived:** | **Mortality:** |
|---|---|---|---|---|---|
| 25 | Nest | *Aloe microstigma* | 3 | 0 | 3 |
| 27 | Nest | *Aloe microstigma* | 15 | 2 | 13 |
| 43 | Nest | *Aloe microstigma* | 14 | 0 | 14 |
| 58 | Nest | *Aloe microstigma* | 14 | 0 | 14 |
| 72 | Nest | *Aloe microstigma* | 7 | 0 | 7 |
| 83 | Nest | *Aloe microstigma* | 4 | 0 | 4 |
| 86 | Nest | *Aloe microstigma* | 7 | 1 | 6 |
| 92 | Nest | *Aloe microstigma* | 12 | 0 | 12 |
| 96 | Nest | *Aloe microstigma* | 6 | 0 | 6 |
| 99 | Nest | *Aloe microstigma* | 13 | 0 | 13 |
| 2 | Nest | *Anginon* sp. | 14 | 0 | 14 |
| 5 | Nest | *Anginon* sp. | 15 | 0 | 15 |
| 10 | Nest | *Anginon* sp. | 8 | 1 | 7 |
| 47 | Nest | *Anginon* sp. | 14 | 0 | 14 |
| 52 | Nest | *Anginon* sp. | 5 | 0 | 5 |
| 53 | Nest | *Anginon* sp. | 17 | 0 | 17 |
| 73 | Nest | *Anginon* sp. | 15 | 1 | 14 |
| 78 | Nest | *Anginon* sp. | 14 | 0 | 14 |
| 82 | Nest | *Anginon* sp. | 13 | 0 | 13 |
| 100 | Nest | *Anginon* sp. | 12 | 0 | 12 |
| 13 | Nest | *Pteronia incana* | 8 | 0 | 8 |
| 18 | Nest | *Pteronia incana* | 3 | 0 | 3 |
| 20 | Nest | *Pteronia incana* | 12 | 0 | 12 |
| 35 | Nest | *Pteronia incana* | 2 | 0 | 2 |
| 36 | Nest | *Pteronia incana* | 5 | 0 | 5 |
| 59 | Nest | *Pteronia incana* | 6 | 0 | 6 |
| 64 | Nest | *Pteronia incana* | 7 | 0 | 7 |
| 94 | Nest | *Pteronia incana* | 8 | 0 | 8 |
| 95 | Nest | *Pteronia incana* | 15 | 1 | 14 |
| 107 | Nest | *Pteronia incana* | 0 | 0 | 0 |
| 28 | Nest | *Pteronia paniculatus* | 15 | 0 | 15 |
| 42 | Nest | *Pteronia paniculatus* | 4 | 0 | 4 |
| 61 | Nest | *Pteronia paniculatus* | 20 | 0 | 20 |
| 76 | Nest | *Pteronia paniculatus* | 1 | 0 | 1 |
| 77 | Nest | *Pteronia paniculatus* | 0 | 0 | 0 |
| 79 | Nest | *Pteronia paniculatus* | 23 | 0 | 23 |

| Pot number: | Soil treatment: | Species: | Total germinated: | Survived: | Mortality: |
|---|---|---|---|---|---|
| 101 | Nest | *Pteronia paniculatus* | 3 | 0 | 3 |
| 104 | Nest | *Pteronia paniculatus* | 1 | 0 | 1 |
| 106 | Nest | *Pteronia paniculatus* | 1 | 0 | 1 |
| 116 | Nest | *Pteronia paniculatus* | 1 | 0 | 1 |
| 14 | Nest | *Ruschia decurvans* | 3 | 0 | 3 |
| 15 | Nest | *Ruschia decurvans* | 2 | 0 | 2 |
| 19 | Nest | *Ruschia decurvans* | 0 | 0 | 0 |
| 26 | Nest | *Ruschia decurvans* | 6 | 0 | 6 |
| 66 | Nest | *Ruschia decurvans* | 1 | 0 | 1 |
| 67 | Nest | *Ruschia decurvans* | 4 | 0 | 4 |
| 71 | Nest | *Ruschia decurvans* | 0 | 0 | 0 |
| 75 | Nest | *Ruschia decurvans* | 0 | 0 | 0 |
| 93 | Nest | *Ruschia decurvans* | 29 | 0 | 29 |
| 112 | Nest | *Ruschia decurvans* | 7 | 0 | 7 |
| 3 | Nest | *Tylecodon paniculata* | 7 | 0 | 7 |
| 9 | Nest | *Tylecodon paniculata* | 7 | 0 | 7 |
| 24 | Nest | *Tylecodon paniculata* | 1 | 0 | 1 |
| 32 | Nest | *Tylecodon paniculata* | 35 | 0 | 35 |
| 38 | Nest | *Tylecodon paniculata* | 13 | 0 | 13 |
| 44 | Nest | *Tylecodon paniculata* | 1 | 0 | 1 |
| 48 | Nest | *Tylecodon paniculata* | 6 | 0 | 6 |
| 54 | Nest | *Tylecodon paniculata* | 8 | 0 | 8 |
| 69 | Nest | *Tylecodon paniculata* | 13 | 0 | 13 |
| 105 | Nest | *Tylecodon paniculata* | 0 | 0 | 0 |
| 7 | Matrix | *Aloe microstigma* | 7 | 0 | 7 |
| 23 | Matrix | *Aloe microstigma* | 9 | 0 | 9 |
| 39 | Matrix | *Aloe microstigma* | 6 | 1 | 5 |
| 45 | Matrix | *Aloe microstigma* | 0 | 0 | 0 |
| 84 | Matrix | *Aloe microstigma* | 7 | 0 | 7 |
| 87 | Matrix | *Aloe microstigma* | 4 | 0 | 4 |
| 98 | Matrix | *Aloe microstigma* | 12 | 0 | 12 |
| 111 | Matrix | *Aloe microstigma* | 1 | 0 | 1 |
| 115 | Matrix | *Aloe microstigma* | 4 | 0 | 4 |
| 117 | Matrix | *Aloe microstigma* | 6 | 0 | 6 |
| 11 | Matrix | *Anginon* sp. | 10 | 0 | 10 |
| 16 | Matrix | *Anginon* sp. | 18 | 0 | 18 |
| 17 | Matrix | *Anginon* sp. | 14 | 0 | 14 |
| 22 | Matrix | *Anginon* sp. | 10 | 0 | 10 |
| 29 | Matrix | *Anginon* sp. | 14 | 0 | 14 |
| 49 | Matrix | *Anginon* sp. | 9 | 0 | 9 |
| 85 | Matrix | *Anginon* sp. | 15 | 0 | 15 |
| 88 | Matrix | *Anginon* sp. | 13 | 1 | 12 |
| 108 | Matrix | *Anginon* sp. | 10 | 0 | 10 |
| 114 | Matrix | *Anginon* sp. | 8 | 0 | 8 |
| 4 | Matrix | *Pteronia incana* | 2 | 0 | 2 |

| Pot number: | Soil treatment: | Species: | Total germinated: | Survived: | Mortality: |
|---|---|---|---|---|---|
| 31 | Matrix | *Pteronia incana* | 1 | 0 | 1 |
| 41 | Matrix | *Pteronia incana* | 2 | 0 | 2 |
| 50 | Matrix | *Pteronia incana* | 2 | 0 | 2 |
| 51 | Matrix | *Pteronia incana* | 1 | 0 | 1 |
| 56 | Matrix | *Pteronia incana* | 3 | 0 | 3 |
| 70 | Matrix | *Pteronia incana* | 0 | 0 | 0 |
| 74 | Matrix | *Pteronia incana* | 1 | 0 | 1 |
| 91 | Matrix | *Pteronia incana* | 1 | 0 | 1 |
| 103 | Matrix | *Pteronia incana* | 0 | 0 | 0 |
| 1 | Matrix | *Pteronia paniculatus* | 0 | 0 | 0 |
| 6 | Matrix | *Pteronia paniculatus* | 5 | 0 | 5 |
| 12 | Matrix | *Pteronia paniculatus* | 4 | 0 | 4 |
| 33 | Matrix | *Pteronia paniculatus* | 5 | 0 | 5 |
| 37 | Matrix | *Pteronia paniculatus* | 3 | 0 | 3 |
| 62 | Matrix | *Pteronia paniculatus* | 0 | 0 | 0 |
| 68 | Matrix | *Pteronia paniculatus* | 2 | 0 | 2 |
| 81 | Matrix | *Pteronia paniculatus* | 0 | 0 | 0 |
| 113 | Matrix | *Pteronia paniculatus* | 3 | 0 | 3 |
| 120 | Matrix | *Pteronia paniculatus* | 4 | 0 | 4 |
| 21 | Matrix | *Ruschia decurvans* | 1 | 0 | 1 |
| 30 | Matrix | *Ruschia decurvans* | 0 | 0 | 0 |
| 46 | Matrix | *Ruschia decurvans* | 0 | 0 | 0 |
| 55 | Matrix | *Ruschia decurvans* | 0 | 0 | 0 |
| 57 | Matrix | *Ruschia decurvans* | 1 | 0 | 1 |
| 97 | Matrix | *Ruschia decurvans* | 0 | 0 | 0 |
| 102 | Matrix | *Ruschia decurvans* | 1 | 0 | 1 |
| 109 | Matrix | *Ruschia decurvans* | 0 | 0 | 0 |
| 110 | Matrix | *Ruschia decurvans* | 0 | 0 | 0 |
| 119 | Matrix | *Ruschia decurvans* | 1 | 0 | 1 |
| 8 | Matrix | *Tylecodon paniculata* | 0 | 0 | 0 |
| 34 | Matrix | *Tylecodon paniculata* | 5 | 0 | 5 |
| 40 | Matrix | *Tylecodon paniculata* | 3 | 0 | 3 |
| 60 | Matrix | *Tylecodon paniculata* | 3 | 0 | 3 |
| 63 | Matrix | *Tylecodon paniculata* | 2 | 0 | 2 |
| 65 | Matrix | *Tylecodon paniculata* | 7 | 0 | 7 |
| 80 | Matrix | *Tylecodon paniculata* | 5 | 2 | 3 |
| 89 | Matrix | *Tylecodon paniculata* | 0 | 0 | 0 |
| 90 | Matrix | *Tylecodon paniculata* | 1 | 0 | 1 |
| 118 | Matrix | *Tylecodon paniculata* | 6 | 1 | 5 |

# Appendix J

The raw data table of independent variables (carbon, calcium, and nitrogen concentration, and mean soil particle size, water holding capacity, water infiltrate time and water retention time) from two habitats (*Microhodotermes viator* nests and the associated matrices).

| **Habitat** | **Carbon (%)** | **Calcium (cmol/mol)** | **Nitrogen (%)** | **Mean soil particle size (µm)** | **Water holding capacity (ml)** | **Water infiltration time (sec.25 ml-1)** | **Retention time** |
|---|---|---|---|---|---|---|---|
| Nest | 4,41 | 7,01 | 0,263 | 160,6 | 105,35 | 262,35 | 23 |
| Nest | 4,41 | 1,7 | 0,255 | 203,1 | 105,55 | 6,02 | 23 |
| Nest | 4,64 | 14,28 | 0,358 | 192,9 | 104,8 | 100,68 | 21 |
| Nest | 8,66 | 17,42 | 0,458 | 216,2 | 129,8 | 234,43 | 21 |
| Nest | 5,38 | 19,12 | 0,344 | 277,9 | 127,45 | 89,2 | 21 |
| Nest | 2,89 | 11,03 | 0,195 | 169,4 | 84,7 | 203,4 | 17 |
| Nest | 2,32 | 3,86 | 0,184 | 133,8 | 91,75 | 39,17 | 15 |
| Nest | 2,16 | 3,75 | 0,163 | 175,5 | 67,7 | 289,83 | 8 |
| Nest | 3,71 | 11,34 | 0,241 | 227,9 | 97,75 | 35,59 | 17 |
| Nest | 3,16 | 3,56 | 0,233 | 208,5 | 97,6 | 9,95 | 17 |
| Nest | 3,24 | 13,29 | 0,227 | 231,7 | 93,95 | 568,41 | 19 |
| Nest | 2,11 | 5,54 | 0,16 | 171,4 | 72,2 | 274,45 | 11 |
| Nest | 1,99 | 3,01 | 0,136 | 209,8 | 79,35 | 31,9 | 8 |
| Nest | 3,86 | 8,94 | 0,253 | 223,7 | 81,75 | 51,98 | 8 |
| Nest | 4,29 | 15,83 | 0,251 | 330,2 | 111,05 | 153,26 | 11 |
| Nest | 3,32 | 4,62 | 0,222 | 166,9 | 90,75 | 44,65 | 13 |
| Nest | 2,89 | 2,6 | 0,183 | 159,1 | 82 | 24,26 | 11 |
| Nest | 1,99 | 5,29 | 0,162 | 164,1 | 74,35 | 58,8 | 11 |
| Nest | 3,9 | 14,57 | 0,278 | 220,1 | 104,55 | 127,68 | 8 |
| Nest | 8,35 | 22,5 | 0,496 | 212,4 | 127,45 | 110,37 | 15 |
| Matrix | 3,86 | 7,5 | 0,21 | 214,7 | 106,9 | 116,56 | 17 |
| Matrix | 1,87 | 10,79 | 0,174 | 157,1 | 100,4 | 989,86 | 17 |
| Matrix | 1,25 | 1,84 | 0,086 | 198,2 | 65,4 | 367,84 | 6 |
| Matrix | 3,16 | 1,46 | 0,139 | 255,2 | 90,4 | 563,45 | 15 |
| Matrix | 2,18 | 1 | 0,173 | 269,5 | 78,55 | 464,16 | 15 |
| Matrix | 1,29 | 1,32 | 0,105 | 195,3 | 59,95 | 1249,84 | 15 |
| Matrix | 2,09 | 2,46 | 0,147 | 201 | 87,8 | 133,84 | 17 |
| Matrix | 5,19 | 7,03 | 0,258 | 359,4 | 94,45 | 1124,35 | 17 |
| Matrix | 1,29 | 1,35 | 0,115 | 314,1 | 80,25 | 1187,9 | 11 |
| Matrix | 1,15 | 1,25 | 0,118 | 139,3 | 58,2 | 1086,31 | 5 |
| Matrix | 3,2 | 1,7 | 0,206 | 267,9 | 94,45 | 1133,41 | 15 |
| Matrix | 3,94 | 5,79 | 0,186 | 258,9 | 92,75 | 64,96 | 8 |
| Matrix | 4,02 | 2,85 | 0,251 | 246,7 | 100,35 | 51,38 | 8 |
| Matrix | 1,91 | 2,32 | 0,107 | 172,2 | 71,2 | 437,29 | 8 |
| Matrix | 2,03 | 0,35 | 0,136 | 286,4 | 65,15 | 202,1 | 11 |
| Matrix | 1,91 | 1,84 | 0,119 | 150,2 | 75 | 15,37 | 6 |
| Matrix | 3,08 | 1,68 | 0,205 | 157,6 | 97,55 | 57,04 | 11 |
| Matrix | 2,96 | 1,66 | 0,18 | 296,4 | 96,1 | 412,9 | 11 |
| Matrix | 3,35 | 4,35 | 0,226 | 173,8 | 103,1 | 287,35 | 8 |
| Matrix | 2,18 | 1,46 | 0,153 | 166,8 | 95,8 | 279,88 | 8 |

# Appendix K

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Correlation (r) and significance (* = $p < 0.05$; ** = $p < 0.01$) matrices of dependent/growth variables and explanatory variables/independent variables in nest (red) and matrix (blue) habitats for *Aloe microstigma*:

| Variable | Value | Root length | Shoot length | Number of leaves | Health | Carbon | Calcium | Nitrogen | Particle size | Water holding capacity | Percolation rate | Retention time |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Root length** | r | 1 | 0,3313 | -0,277 | 0,2296 | -0,0682 | -0,1965 | 0,0183 | -0,0217 | 0,026 | 0,2907 | -0,1748 |
| | p-value | N/A | 0,1658 | 0,251 | 0,3444 | 0,7814 | 0,4201 | 0,9407 | 0,9298 | 0,916 | 0,2273 | 0,4741 |
| **Shoot length** | r | -0,1873 | 1 | **0,4683** | -0,0928 | -0,028 | -0,4478 | -0,1218 | -0,0997 | -0,0673 | -0,1905 | -0,3627 |
| | p-value | 0,4717 | N/A | **0,0431*** | 0,7058 | 0,9093 | 0,545 | 0,6195 | 0,6846 | 0,7844 | 0,4347 | 0,1269 |
| **Number of leaves** | r | -0,1532 | **0,6014** | 1 | -0,1437 | 0,0411 | 0,0775 | -0,0119 | -0,2362 | 0,0128 | -0,3343 | -0,2749 |
| | p-value | 0,0557 | **0,0107*** | N/A | 0,5572 | 0,8674 | 0,7524 | 0,9616 | 0,3303 | 0,9586 | 0,1618 | 0,2548 |
| **Health** | r | -0,0263 | 0,0583 | -0,0752 | 1 | -0,2098 | -0,1541 | -0,2023 | 0,0767 | -0,4447 | **0,5999** | 0,0774 |
| | p-value | 0,9203 | 0,8242 | 0,7742 | N/A | 0,3886 | 0,5289 | 0,4062 | 0,7549 | 0,0564 | **0,0066**** | 0,7529 |
| **Carbon** | r | -0,0527 | 0,3129 | **0,6429** | -0,0338 | 1 | 0,3989 | **0,8995** | 0,448 | **0,7301** | -0,1736 | 0,3597 |
| | p-value | 0,8407 | 0,2214 | **0,0054**** | 0,8976 | N/A | 0,0907 | **0,0000**** | 0,0544 | **0,0004**** | 0,4773 | 0,1304 |
| **Calcium** | r | -0,3498 | 0,4026 | **0,6499** | 0,1835 | **0,7861** | 1 | **0,4686** | -0,0535 | **0,5478** | 0,1394 | **0,0464** |
| | p-value | 0,1688 | 0,1091 | **0,0047**** | 0,4808 | **0,0002**** | N/A | **0,043*** | 0,8278 | **0,0152*** | 0,5693 | **0,0456*** |
| **Nitrogen** | r | -0,077 | 0,448 | **0,7519** | -0,0561 | **0,9723** | **0,8237** | 1 | 0,3268 | **0,8001** | -0,1286 | 0,3399 |
| | p-value | 0,7691 | 0,0713 | **0,0005**** | 0,8306 | **0,0000**** | **0,0000**** | N/A | 0,1721 | **0,0000**** | 0,5999 | 0,1545 |
| **Particle size** | r | -0,288 | -0,1956 | 0,1856 | 0,0652 | 0,369 | **0,5174** | 0,3199 | 1 | 0,1317 | 0,2838 | 0,4164 |
| | p-value | 0,2624 | 0,4517 | 0,4757 | 0,8036 | 0,1449 | **0,0334*** | 0,2136 | N/A | 0,591 | 0,239 | 0,0762 |
| **Water holding capacity** | r | -0,1649 | 0,2875 | **0,5843** | -0,0005 | **0,901** | **0,7449** | **0,8921** | **0,4852** | 1 | -0,2647 | 0,3744 |
| | p-value | 0,527 | 0,2632 | **0,0138*** | 0,9984 | **0,0000**** | **0,0006**** | **0,0000**** | **0,0483*** | N/A | 0,2735 | 0,1143 |
| **Percolation rate** | r | 0,3533 | -0,1192 | 0,1292 | 0,1811 | 0,1406 | 0,325 | 0,1122 | 0,0439 | -0,0534 | 1 | 0,2914 |
| | p-value | 0,1642 | 0,6487 | 0,621 | 0,4866 | 0,5904 | 0,2031 | 0,6681 | 0,8671 | 0,8388 | N/A | 0,2262 |
| **Retention time** | r | 0,0023 | 0,0478 | 0,4679 | 0,1059 | **0,4857** | 0,1901 | **0,4951** | -0,0478 | **0,578** | -0,1315 | 1 |
| | p-value | 0,9929 | 0,8554 | 0,0582 | 0,6858 | **0,0481*** | 0,4649 | **0,0433*** | 0,8555 | **0,0151**** | 0,6149 | N/A |

Correlation (r) and significance (* = $p < 0.05$; ** = $p < 0.01$) matrices of dependent/growth variables and explanatory variables/independent variables in nest (red) and matrix (blue) habitats for *Pteronia incana*:

| Variable | Value | Root length | Shoot length | Number of leaves | Health | Carbon | Calcium | Nitrogen | Particle size | Water holding capacity | Percolation rate | Retention time |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Root length** | r | 1 | 0,4277 | 0,605 | 0,5415 | 0,3537 | 0,5227 | 0,3608 | 0,2715 | 0,214 | 0,6695 | 0,2363 |
| | p-value | N/A | 0,0868 | 0,0101* | 0,0248* | 0,1637 | 0,0313 | 0,1548 | 2918 | 0,4095 | 0,0033 | 0,3612 |
| **Shoot length** | r | 0,3231 | 1 | 0,7707 | -0,1236 | 0,1833 | 0,2989 | 0,185 | -0,0213 | -0,0593 | 0,2772 | 0,0517 |
| | p-value | 0,1772 | N/A | 0,0003** | 0,6366 | 0,4814 | 0,2438 | 0,4772 | 0,9352 | 0,8212 | 0,2815 | 0,8438 |
| **Number of leaves** | r | 0,2911 | 0,8472 | 1 | 0,0442 | 0,2868 | 0,4422 | 0,2557 | 0,269 | 0,2097 | 0,2815 | 0,1416 |
| | p-value | 0,2266 | 0,0000** | N/A | 0,8661 | 0,2645 | 0,0755 | 0,3219 | 0,2964 | 0,4191 | 0,2736 | 0,5878 |
| **Health** | r | 0,6259 | 0,0604 | 0,0645 | 1 | 0,2932 | 0,2883 | 0,2782 | -0,0007 | 0,2094 | 0,476 | 0,1139 |
| | p-value | 0,0041** | 0,8061 | 0,7924 | N/A | 0,2535 | 0,2618 | 0,2797 | 0,9978 | 0,4199 | 0,0534 | 0,6634 |
| **Carbon** | r | 0,4438 | -0,1486 | -0,1104 | 0,3664 | 1 | 0,3989 | 0,8995 | 0,448 | 0,7301 | -0,1736 | 0,3597 |
| | p-value | 0,057 | 0,5437 | 0,6528 | 0,1229 | N/A | 0,0907 | 0,0000** | 0,0544 | 0,0004** | 0,4773 | 0,1304 |
| **Calcium** | r | -0,1657 | -0,289 | -0,1575 | 0,3243 | 0,7861 | 1 | 0,4686 | -0,0535 | 0,5478 | 0,1394 | 0,0464 |
| | p-value | 0,4978 | 0,2302 | 0,5197 | 0,0176 | 0,0002** | N/A | 0,043* | 0,8278 | 0,0152* | 0,5693 | 0,0456* |
| **Nitrogen** | r | 0,2974 | 0,0062 | 0,123 | 0,2382 | 0,9723 | 0,8237 | 1 | 0,3268 | 0,8001 | -0,1286 | 0,3399 |
| | p-value | 0,2162 | 0,9798 | 0,6159 | 0,3262 | 0,0000** | 0,0000** | N/A | 0,1721 | 0,0000** | 0,5999 | 0,1545 |
| **Particle size** | r | 0,2419 | -0,0268 | -0,1242 | 0,1853 | 0,369 | 0,5174 | 0,3199 | 1 | 0,1317 | 0,2838 | 0,4164 |
| | p-value | 0,3184 | 0,9133 | 0,6125 | 0,4477 | 0,1449 | 0,0334* | 0,2136 | N/A | 0,591 | 0,239 | 0,0762 |
| **Water holding capacity** | r | 0,115 | -0,2061 | 0,0254 | 0,2579 | 0,901 | 0,7449 | 0,8921 | 0,4852 | 1 | -0,2647 | 0,3744 |
| | p-value | 0,6391 | 0,3973 | 0,9177 | 0,2864 | 0,0000** | 0,0006** | 0,0000** | 0,0483* | N/A | 0,2735 | 0,1143 |
| **Percolation rate** | r | -0,1723 | -0,0363 | -0,117 | 0,0695 | 0,1406 | 0,325 | 0,1122 | 0,0439 | -0,0534 | 1 | 0,2914 |
| | p-value | 0,4806 | 0,8827 | 0,6333 | 0,7774 | 0,5904 | 0,2031 | 0,6681 | 0,8671 | 0,8388 | N/A | 0,2262 |
| **Retention time** | r | -0,1025 | -0,4671 | -0,3789 | 0,1316 | 0,4857 | 0,1901 | 0,4951 | -0,0478 | 0,578 | -0,1315 | 1 |
| | p-value | 0,6761 | 0,0438* | 0,1097 | 0,5911 | 0,0481* | 0,4649 | 0,0433* | 0,8555 | 0,0151** | 0,6149 | N/A |

Correlation (r) and significance (* = $p < 0.05$; ** = $p < 0.01$) matrices of dependent/growth variables and explanatory variables/independent variables in nest (red) and matrix (blue) habitats for *Pteronia paniculata*:

| **Variable** | **Value** | **Root length** | **Shoot length** | **Number of leaves** | **Health** | **Carbon** | **Calcium** | **Nitrogen** | **Particle size** | **Water holding capacity** | **Percolation rate** | **Retention time** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Root length** | r | 1 | 0,4645 | **0,7191** | 0-<br>0,28659818 | 0,3127 | 0,3176 | 0,356 | 0,0762 | 0,2205 | 0,5253 | 0,0846 |
| | p-value | N/A | 0,0603 | **0,0011*** | 0,2647 | 0,2217 | 0,2141 | 0,1604 | 0,7714 | 0,395 | 0,0304 | 0,7469 |
| **Shoot length** | r | -0,1062 | 1 | 0,4665 | -0,3062 | 0,4344 | 0,5096 | **0,4853** | 0,0613 | 0,3801 | 0,3843 | 0,3928 |
| | p-value | 0,6653 | N/A | 0,0591 | 0,2319 | 0,0815 | 0,0367 | **0,0483*** | 0,8151 | 0,1234 | 0,1277 | 0,1189 |
| **Number of leaves** | r | 0,1215 | **0,5768** | 1 | 0,0019 | 0,3596 | 0,3428 | 0,4108 | -0,0536 | 0,2857 | 0,208 | 0,0454 |
| | p-value | 0,6201 | **0,0097**** | N/A | 0,9943 | 0,1562 | 0,178 | 0,1014 | 0,8382 | 0,2662 | 0,423 | 0,8626 |
| **Health** | r | **0,6258** | -0,3892 | -0,2274 | 1 | 0 | 0,0427 | 0,0112 | -0,069 | -0,0208 | -0,1129 | -0,2271 |
| | p-value | **0,0042**** | 0,0995 | 0,3491 | N/A | 0,9999 | 0,8708 | 0,966 | 0,7924 | 0,9367 | 0,6661 | 0,3808 |
| **Carbon** | r | -0,0126 | 0,2264 | -0,027 | -0,251 | 1 | 0,3989 | **0,8995** | 0,448 | **0,7301** | -0,1736 | 0,3597 |
| | p-value | 0,9592 | 0,3514 | 0,9128 | 0,3 | N/A | 0,0907 | **0,0000**** | 0,0544 | **0,0004**** | 0,4773 | 0,1304 |
| **Calcium** | r | -0,1593 | 0,2279 | -0,0507 | -0,1 | **0,7861** | 1 | **0,4686** | -0,0535 | **0,5478** | 0,1394 | **0,0464** |
| | p-value | 0,5147 | 0,3481 | 0,8367 | 0,6837 | **0,0002**** | N/A | **0,043*** | 0,8278 | **0,0152*** | 0,5693 | **0,0456*** |
| **Nitrogen** | r | -0,0791 | 0,0807 | -0,0671 | -0,22 | **0,9723** | **0,8237** | 1 | 0,3268 | **0,8001** | -0,1286 | 0,3399 |
| | p-value | 0,7474 | 0,7427 | 0,7849 | 0,3655 | **0,0000**** | **0,0000**** | N/A | 0,1721 | **0,0000**** | 0,5999 | 0,1545 |
| **Particle size** | r | 0,1476 | -0,2642 | -0,2407 | 0,2647 | 0,369 | **0,5174** | 0,3199 | 1 | 0,1317 | 0,2838 | 0,4164 |
| | p-value | 0,5465 | 0,2743 | 0,3209 | 0,2734 | 0,1449 | **0,0334*** | 0,2136 | N/A | 0,591 | 0,239 | 0,0762 |
| **Water holding capacity** | r | -0,1775 | 0,3883 | 0,2184 | -0,2279 | **0,901** | **0,7449** | **0,8921** | **0,4852** | 1 | -0,2647 | 0,3744 |
| | p-value | 0,4672 | 0,1004 | 0,3691 | 0,348 | **0,0000**** | **0,0006**** | **0,0000**** | **0,0483*** | N/A | 0,2735 | 0,1143 |
| **Percolation rate** | r | 0,3959 | -0,1747 | -0,2398 | 0,5385 | 0,1406 | 0,325 | 0,1122 | 0,0439 | -0,0534 | 1 | 0,2914 |
| | p-value | 0,0934 | 0,4744 | 0,3228 | 0,0174 | 0,5904 | 0,2031 | 0,6681 | 0,8671 | 0,8388 | N/A | 0,2262 |
| **Retention time** | r | -0,0618 | 0,0196 | -0,0973 | 0,1113 | **0,4857** | 0,1901 | **0,4951** | -0,0478 | **0,578** | -0,1315 | 1 |
| | p-value | 0,8015 | 0,9364 | 0,6919 | 0,65 | **0,0481*** | 0,4649 | **0,0433*** | 0,8555 | **0,0151**** | 0,6149 | N/A |

Correlation (r) and significance (* = $p < 0.05$; ** = $p < 0.01$) matrices of dependent/growth variables and explanatory variables/independent variables in nest (red) and matrix (blue) habitats for *Tylecodon paniculata*:

| Variable | Value | Root length | Shoot length | Number of leaves | Health | Carbon | Calcium | Nitrogen | Particle size | Water holding capacity | Percolation rate | Retention time |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Root length** | r | 1 | -0,1873 | -0,1532 | -0,0263 | 0,0527 | -0,3498 | -0,077 | -0,288 | -0,1649 | 0,3533 | 0,0023 |
| | p-value | N/A | 0,4717 | 0,5572 | 0,9203 | 0,8407 | 0,1688 | 0,7691 | 0,2624 | 0,527 | 0,1642 | 0,9929 |
| **Shoot length** | r | 0,3313 | 1 | **0,6014** | 0,0583 | 0,3129 | 0,4026 | 0,448 | -0,1956 | 0,2875 | -0,1192 | 0,0478 |
| | p-value | 0,1658 | N/A | **0,0107*** | 0,8242 | 0,2214 | 0,1091 | 0,0713 | 0,4517 | 0,2632 | 0,6487 | 0,8554 |
| **Number of leaves** | r | -0,277 | **0,4683** | 1 | -0,0752 | **0,6429** | **0,6499** | **0,7519** | 0,1856 | **0,5843** | 0,1292 | 0,4679 |
| | p-value | 0,251 | **0,0431*** | N/A | 0,7742 | **0,0054**** | **0,0047**** | **0,0005**** | 0,4757 | **0,0138*** | 0,621 | 0,0582 |
| **Health** | r | 0,2296 | -0,0927 | -0,1437 | 1 | -0,0338 | 0,1835 | -0,0561 | 0,0652 | -0,0005 | 0,1811 | 0,1059 |
| | p-value | 0,3444 | 0,7058 | 0,5572 | N/A | 0,8976 | 0,4808 | 0,8306 | 0,8036 | 0,9984 | 0,4866 | 0,6858 |
| **Carbon** | r | -0,0682 | -0,028 | 0,0411 | -0,2098 | 1 | 0,3989 | **0,8995** | 0,448 | **0,7301** | -0,1736 | 0,3597 |
| | p-value | 0,7814 | 0,9093 | 0,8674 | 0,3886 | N/A | 0,0907 | **0,0000**** | 0,0544 | **0,0004**** | 0,4773 | 0,1304 |
| **Calcium** | r | -0,1965 | -0,4478 | 0,0775 | -0,1541 | **0,7861** | 1 | **0,4686** | -0,0535 | **0,5478** | 0,1394 | **0,0464** |
| | p-value | 0,4201 | 0,0545 | 0,7524 | 0,5289 | **0,0002**** | N/A | **0,043*** | 0,8278 | **0,0152*** | 0,5693 | **0,0456*** |
| **Nitrogen** | r | 0,0183 | -0,1218 | -0,0119 | -0,2023 | **0,9723** | **0,8237** | 1 | 0,3268 | **0,8001** | -0,1286 | 0,3399 |
| | p-value | 0,9407 | 0,6195 | 0,9616 | 0,4062 | **0,0000**** | **0,0000**** | N/A | 0,1721 | **0,0000**** | 0,5999 | 0,1545 |
| **Particle size** | r | -0,0217 | -0,0997 | -0,2362 | 0,0767 | 0,369 | **0,5174** | 0,3199 | 1 | 0,1317 | 0,2838 | 0,4164 |
| | p-value | 0,9298 | 0,6846 | 0,3303 | 0,7549 | 0,1449 | **0,0334*** | 0,2136 | N/A | 0,591 | 0,239 | 0,0762 |
| **Water holding capacity** | r | 0,026 | -0,0673 | 0,0128 | 0,4447 | **0,901** | **0,7449** | **0,8921** | **0,4852** | 1 | -0,2647 | 0,3744 |
| | p-value | 0,916 | 0,7844 | 0,9586 | 0,0564 | **0,0000**** | **0,0006**** | **0,0000**** | **0,0483*** | N/A | 0,2735 | 0,1143 |
| **Percolation rate** | r | 0,2907 | -0,1905 | -0,3343 | **0,5999** | 0,1406 | 0,325 | 0,1122 | 0,0439 | -0,0534 | 1 | 0,2914 |
| | p-value | 0,2273 | 0,4347 | 0,1618 | **0,0066**** | 0,5904 | 0,2031 | 0,6681 | 0,8671 | 0,8388 | N/A | 0,2262 |
| **Retention time** | r | -0,1748 | -0,3627 | -0,2749 | 0,0774 | **0,4857** | 0,1901 | **0,4951** | -0,0478 | **0,578** | -0,1315 | 1 |
| | p-value | 0,4741 | 0,1269 | 0,2548 | 0,7529 | **0,0481*** | 0,4649 | **0,0433*** | 0,8555 | **0,0151**** | 0,6149 | N/A |

# Appendix L

The raw data table for the measured dependent variables (difference in root length, shoot length, and number of leaves or branches – depending on the species) including health scores from the in situ reciprocal transplant experiment in two habitats (*Microhodotermes viator* nests and the associated matrices).

| Species | Habitat | Difference in root length | Difference in shoot length | Difference in number of leaves/branches | Health score |
|---|---|---|---|---|---|
| *Aloe microstigma* | Nest | 51,36 | -34,26 | 1 | 1 |
| *Aloe microstigma* | Nest | -98,85 | 2,09 | 4 | 1 |
| *Aloe microstigma* | Nest | 28,14 | -32,99 | 1 | 1 |
| *Aloe microstigma* | Nest | -16,59 | -18,83 | 0 | 5 |
| *Aloe microstigma* | Nest | -45,1 | 5,85 | 0 | 1 |
| *Aloe microstigma* | Nest | 83,07 | -6,99 | 1 | 1 |
| *Aloe microstigma* | Nest | -100,7 | -19,52 | 1 | 1 |
| *Aloe microstigma* | Nest | -45,64 | -5,43 | 0 | 2 |
| *Aloe microstigma* | Nest | -17,58 | -39,4 | 0 | 1 |
| *Aloe microstigma* | Nest | -23,29 | -29,27 | -1 | 2 |
| *Aloe microstigma* | Nest | -38,21 | -25,05 | 0 | 1 |
| *Aloe microstigma* | Nest | -63,29 | -32,85 | 1 | 2 |
| *Aloe microstigma* | Nest | -0,29 | -20,7 | 0 | 1 |
| *Aloe microstigma* | Nest | -5,78 | -23,37 | 0 | 1 |
| *Aloe microstigma* | Nest | -40,15 | -0,67 | 0 | 1 |
| *Aloe microstigma* | Nest | -70,17 | -7,52 | 0 | 1 |
| *Aloe microstigma* | Matrix | -21,84 | 51,81 | 4 | 2 |
| *Aloe microstigma* | Matrix | -78,83 | -35,25 | 3 | 1 |
| *Aloe microstigma* | Matrix | -43,39 | -63,66 | -1 | 1 |
| *Aloe microstigma* | Matrix | -49,46 | -14,31 | 4 | 2 |
| *Aloe microstigma* | Matrix | -54,88 | 7,75 | 1 | 1 |
| *Aloe microstigma* | Matrix | -57 | 1,27 | 1 | 1 |
| *Aloe microstigma* | Matrix | -1,5 | -5,92 | 0 | 5 |
| *Aloe microstigma* | Matrix | -28,11 | -25,86 | 1 | 1 |
| *Aloe microstigma* | Matrix | 4,17 | -16,49 | 0 | 2 |
| *Aloe microstigma* | Matrix | 12,59 | -8,35 | 0 | 2 |
| *Aloe microstigma* | Matrix | -1,36 | -21,84 | 1 | 2 |
| *Aloe microstigma* | Matrix | -25,44 | -29,72 | -1 | 2 |
| *Aloe microstigma* | Matrix | -59,29 | -44,66 | 0 | 2 |
| *Aloe microstigma* | Matrix | -68,72 | -4,31 | 1 | 1 |
| *Aloe microstigma* | Matrix | -67,07 | -21,8 | 0 | 1 |
| *Aloe microstigma* | Matrix | -5,33 | 3,34 | 1 | 1 |
| *Aloe microstigma* | Matrix | 24,05 | -2,28 | 0 | 1 |
| *Aloe microstigma* | Matrix | 15,13 | -7,43 | 0 | 1 |
| *Aloe microstigma* | Matrix | -18,52 | 47,2 | 6 | 1 |

| **Species** | **Habitat** | **Difference in root length** | **Difference in shoot length** | **Difference in number of leaves/branches** | **Health score** |
|---|---|---|---|---|---|
| *Aloe microstigma* | Matrix | 13,87 | 12,71 | -1 | 1 |
| *Pteronia incana* | Nest | -8,77 | -79,11 | -4 | 5 |
| *Pteronia incana* | Nest | 2,65 | -3,03 | 1 | 4 |
| *Pteronia incana* | Nest | -8,09 | -26,31 | 2 | 5 |
| *Pteronia incana* | Nest | 98,63 | 35,77 | 24 | 5 |
| *Pteronia incana* | Nest | -104,6 | -108,8 | -5 | 5 |
| *Pteronia incana* | Nest | 21,39 | -35,15 | 0 | 4 |
| *Pteronia incana* | Nest | -41,9 | -45,9 | 0 | 1 |
| *Pteronia incana* | Nest | -68,9 | -44,41 | 5 | 1 |
| *Pteronia incana* | Nest | 32,35 | -16,56 | 4 | 5 |
| *Pteronia incana* | Nest | -113,9 | -16,12 | 4 | 1 |
| *Pteronia incana* | Nest | -2,55 | -34,82 | -1 | 5 |
| *Pteronia incana* | Nest | 14,34 | -36,36 | 16 | 4 |
| *Pteronia incana* | Nest | -93,4 | -54,59 | -4 | 1 |
| *Pteronia incana* | Nest | -127,67 | -18,32 | -1 | 4 |
| *Pteronia incana* | Nest | -96,7 | 7,18 | 1 | 1 |
| *Pteronia incana* | Nest | -50,3 | -110,1 | -14 | 5 |
| *Pteronia incana* | Nest | 41,36 | 30,42 | 23 | 4 |
| *Pteronia incana* | Matrix | -32 | -115 | -6 | 5 |
| *Pteronia incana* | Matrix | -137,62 | -89,6 | -2 | 5 |
| *Pteronia incana* | Matrix | 3,74 | -12,23 | 5 | 5 |
| *Pteronia incana* | Matrix | -49,36 | -146,78 | -13 | 5 |
| *Pteronia incana* | Matrix | -88 | -32,25 | 8 | 1 |
| *Pteronia incana* | Matrix | -6 | -1,73 | 3 | 5 |
| *Pteronia incana* | Matrix | -45,9 | -44,68 | -3 | 1 |
| *Pteronia incana* | Matrix | 48,48 | -45,01 | -2 | 5 |
| *Pteronia incana* | Matrix | -118,6 | -30,63 | 0 | 1 |
| *Pteronia incana* | Matrix | -77,3 | -52,53 | -2 | 1 |
| *Pteronia incana* | Matrix | -6,15 | -26,22 | 0 | 5 |
| *Pteronia incana* | Matrix | 11,01 | -19,8 | 1 | 5 |
| *Pteronia incana* | Matrix | -2,33 | -28,51 | 0 | 5 |
| *Pteronia incana* | Matrix | 16,38 | -14,88 | 0 | 5 |
| *Pteronia incana* | Matrix | -111 | -22,7 | -2 | 1 |
| *Pteronia incana* | Matrix | -37,5 | -70,2 | 1 | 1 |
| *Pteronia incana* | Matrix | 3,32 | -18,24 | 5 | 5 |
| *Pteronia incana* | Matrix | -2,37 | 73,58 | 16 | 5 |
| *Pteronia incana* | Matrix | 58,17 | -28,12 | 8 | 5 |
| *Pteronia paniculata* | Nest | -54,76 | -62,81 | -2 | 5 |
| *Pteronia paniculata* | Nest | -5,6 | -21,59 | 1 | 5 |
| *Pteronia paniculata* | Nest | 3,77 | -5,87 | 2 | 4 |
| *Pteronia paniculata* | Nest | -38,67 | -23,82 | 5 | 5 |
| *Pteronia paniculata* | Nest | -24 | -11,5 | 5 | 5 |
| *Pteronia paniculata* | Nest | 12 | -30,79 | 6 | 5 |

| **Species** | **Habitat** | **Difference in root length** | **Difference in shoot length** | **Difference in number of leaves/branches** | **Health score** |
|---|---|---|---|---|---|
| *Pteronia paniculata* | Nest | -55,6 | -13,98 | -4 | 3 |
| *Pteronia paniculata* | Nest | 19,15 | -38,33 | 10 | 3 |
| *Pteronia paniculata* | Nest | 15,51 | -25,9 | 2 | 3 |
| *Pteronia paniculata* | Nest | -51,09 | -63,2 | 0 | 5 |
| *Pteronia paniculata* | Nest | -51,8 | -46,7 | 0 | 5 |
| *Pteronia paniculata* | Nest | 0,25 | -49,86 | 2 | 5 |
| *Pteronia paniculata* | Nest | -42,2 | -54,6 | 0 | 5 |
| *Pteronia paniculata* | Nest | -38,16 | -133 | 0 | 5 |
| *Pteronia paniculata* | Nest | -17 | -60,5 | 0 | 5 |
| *Pteronia paniculata* | Nest | -46,4 | -70,65 | 0 | 5 |
| *Pteronia paniculata* | Nest | 25,58 | 8,24 | 17 | 5 |
| *Pteronia paniculata* | Matrix | -60 | 8,89 | 3 | 1 |
| *Pteronia paniculata* | Matrix | -14,44 | -31,67 | 7 | 5 |
| *Pteronia paniculata* | Matrix | 11,57 | -58,89 | -7 | 5 |
| *Pteronia paniculata* | Matrix | 52,38 | 1,61 | 9 | 5 |
| *Pteronia paniculata* | Matrix | -42 | -92 | -4 | 5 |
| *Pteronia paniculata* | Matrix | 7,6 | -7,93 | 0 | 5 |
| *Pteronia paniculata* | Matrix | -80 | -36,11 | 4 | 1 |
| *Pteronia paniculata* | Matrix | 43,55 | -41,35 | 0 | 4 |
| *Pteronia paniculata* | Matrix | 20,14 | -43,63 | 0 | 5 |
| *Pteronia paniculata* | Matrix | 23,08 | -50,24 | -1 | 3 |
| *Pteronia paniculata* | Matrix | 14,38 | -57,61 | 0 | 5 |
| *Pteronia paniculata* | Matrix | -55,5 | -21,79 | 2 | 1 |
| *Pteronia paniculata* | Matrix | -86,1 | -11,19 | 9 | 1 |
| *Pteronia paniculata* | Matrix | 30,94 | -56,06 | 8 | 4 |
| *Pteronia paniculata* | Matrix | -7,74 | -39,85 | 5 | 4 |
| *Pteronia paniculata* | Matrix | 33,56 | -37,35 | 5 | 3 |
| *Pteronia paniculata* | Matrix | -57,13 | -20,97 | 3 | 4 |
| *Pteronia paniculata* | Matrix | -14,6 | -14,25 | -2 | 4 |
| *Pteronia paniculata* | Matrix | 25,31 | 15,76 | 37 | 3 |
| *Tylecodon paniculatus* | Nest | -2,44 | 2,87 | 0 | 1 |
| *Tylecodon paniculatus* | Nest | -51 | -36 | -3 | 5 |
| *Tylecodon paniculatus* | Nest | -10,98 | 0,95 | 0 | 2 |
| *Tylecodon paniculatus* | Nest | -5,42 | -3,3 | 0 | 2 |
| *Tylecodon paniculatus* | Nest | -35,4 | -44,1 | -3 | 5 |
| *Tylecodon paniculatus* | Nest | -11,75 | -22,6 | 0 | 1 |
| *Tylecodon paniculatus* | Nest | 2,54 | -9,07 | 1 | 2 |
| *Tylecodon paniculatus* | Nest | -20,1 | -38,2 | -3 | 5 |
| *Tylecodon paniculatus* | Nest | -11,8 | -39,9 | -3 | 5 |
| *Tylecodon paniculatus* | Nest | -17,5 | -44,2 | -3 | 5 |
| *Tylecodon paniculatus* | Nest | -16,28 | -12,57 | 3 | 1 |
| *Tylecodon paniculatus* | Nest | 7,44 | -7,33 | 0 | 2 |
| *Tylecodon paniculatus* | Nest | -24,2 | -31,1 | -3 | 5 |

| Species | Habitat | Difference in root length | Difference in shoot length | Difference in number of leaves/branches | Health score |
|---|---|---|---|---|---|
| *Tylecodon paniculatus* | Nest | 9,04 | -1,34 | -1 | 1 |
| *Tylecodon paniculatus* | Nest | 0,71 | 8,4 | 1 | 1 |
| *Tylecodon paniculatus* | Nest | -2,31 | -7,12 | -1 | 1 |
| *Tylecodon paniculatus* | Nest | -24 | -24 | -3 | 5 |
| *Tylecodon paniculatus* | Matrix | -14,45 | -21,69 | 0 | 1 |
| *Tylecodon paniculatus* | Matrix | -18,37 | -8,32 | 3 | 2 |
| *Tylecodon paniculatus* | Matrix | -9,15 | -9,23 | 0 | 3 |
| *Tylecodon paniculatus* | Matrix | -14,59 | 1,56 | -1 | 1 |
| *Tylecodon paniculatus* | Matrix | 19,64 | -3,5 | 0 | 3 |
| *Tylecodon paniculatus* | Matrix | 8,38 | -21,47 | 4 | 1 |
| *Tylecodon paniculatus* | Matrix | -63,72 | -43,89 | 0 | 3 |
| *Tylecodon paniculatus* | Matrix | -8,35 | -19,74 | 0 | 2 |
| *Tylecodon paniculatus* | Matrix | -17 | -50,5 | -5 | 5 |
| *Tylecodon paniculatus* | Matrix | -16,8 | -61,2 | -4 | 5 |
| *Tylecodon paniculatus* | Matrix | -8,76 | -14,62 | 0 | 2 |
| *Tylecodon paniculatus* | Matrix | 5,03 | 1,28 | -1 | 3 |
| *Tylecodon paniculatus* | Matrix | -3,17 | -4,1 | 2 | 2 |
| *Tylecodon paniculatus* | Matrix | -17,5 | -45,8 | -2 | 5 |
| *Tylecodon paniculatus* | Matrix | -26,2 | -48,8 | -4 | 5 |
| *Tylecodon paniculatus* | Matrix | -4,81 | 0,11 | 0 | 2 |
| *Tylecodon paniculatus* | Matrix | -16 | -18 | -4 | 5 |
| *Tylecodon paniculatus* | Matrix | -23 | -31 | -3 | 5 |

# Appendix M

The plant species key, whereby each species is assigned a number, to identify plant species found and their cover at each site.

| | |
|---|---|
| *Adenogramma glomerata* | **Sp.1** |
| *Agapanthus praecox* | **Sp.2** |
| *Agathosma ciliaris* | **Sp.3** |
| *Galenia africana* | **Sp.4** |
| *Aizoon sarcophyllum* | **Sp.5** |
| *Aizoon* sp. | **Sp.6** |
| *Albuca canadensis* | **Sp.7** |
| *Albuca cooperi* | **Sp.8** |
| *Albuca* sp. | **Sp.9** |
| *Allium dregeanum* | **Sp.10** |
| *Aloe microstigma* | **Sp.11** |
| *Ammocharis coranica* | **Sp.12** |
| *Anthospermum aethiopicum* | **Sp.13** |
| *Antimima aristulata* | **Sp.14** |
| *Arctopus echinatus* | **Sp.15** |
| *Arctotheca calendula* | **Sp.16** |
| *Arctotheca* sp. | **Sp.17** |
| *Arctotis acaulis* | **Sp.18** |
| *Arctotis breviscapa* | **Sp.19** |
| *Arctotis* sp. | **Sp.20** |
| *Arctotis stoechadifolia* | **Sp.21** |
| *Argyrolobium tomentosum* | **Sp.22** |
| *Aristea africana* | **Sp.23** |
| *Aristida* sp. | **Sp.24** |
| *Aspalathus cephalotes* | **Sp.25** |
| *Aspalathus ciliaris* | **Sp.26** |
| *Aspalathus cordata* | **Sp.27** |
| *Aspalathus quinquefolia* | **Sp.28** |
| *Aspalathus rubiginosa* | **Sp.29** |
| *Aspalathus* sp. | **Sp.30** |
| *Aspalathus spicata* | **Sp.31** |
| *Aspalathus spinosa* | **Sp.32** |
| *Aspalathus ternatus* | **Sp.33** |
| *Asparagus aethiopicus* | **Sp.34** |
| *Asparagus asparagoides* | **Sp.35** |
| *Asparagus burchelli* | **Sp.36** |
| *Asparagus capensis* | **Sp.37** |
| *Asparagus recurvispinus* | **Sp.38** |
| *Asparagus rubicundus* | **Sp.39** |
| *Asparagus setaceus* | **Sp.40** |
| *Athanasia trifurcata* | **Sp.41** |
| *Atriplex lindleyi* | **Sp.42** |
| *Atriplex semibaccata* | **Sp.43** |
| *Augea capensis* | **Sp.44** |
| *Avena fatua* | **Sp.45** |
| *Babiana ambigua* | **Sp.46** |
| *Babiana fragrans* | **Sp.47** |
| *Babiana* sp. | **Sp.48** |
| *Berkheya armata* | **Sp.49** |
| *Blechnum australe* | **Sp.50** |
| *Briza maxima* | **Sp.51** |
| *Bromus diandrus* | **Sp.52** |
| *Bromus hordeaceus* | **Sp.53** |
| *Bromus pectinatus* | **Sp.54** |
| *Bulbine annua* | **Sp.55** |
| *Bulbine foleyi* | **Sp.56** |
| *Carissa bispinosa* | **Sp.57** |
| *Carpobrotus* sp. | **Sp.58** |
| *Cerastrium glomeratum* | **Sp.59** |
| *Chaenorhinum minus* | **Sp.60** |
| *Cheilanthes sieberi* | **Sp.61** |
| *Cheilanthes* sp. | **Sp.62** |
| *Chlorophytum graminifolium* | **Sp.63** |
| *Chlorophytum triflorum* | **Sp.64** |
| *Chrysocoma ciliata* | **Sp.65** |
| *Cissampelos capensis* | **Sp.66** |
| *Cleretum bellidiforme* | **Sp.67** |
| *Cliffortia atrata* | **Sp.68** |
| *Cliffortia ruscifolia* | **Sp.69** |
| *Clutia laxa* | **Sp.70** |
| *Clutia polifolia* | **Sp.71** |
| *Convolvulus capensis* | **Sp.72** |
| *Coprosma repens* | **Sp.73** |
| *Cortaderia selloana* | **Sp.74** |
| *Cotula* sp. | **Sp.75** |
| *Cotula turbinata* | **Sp.76** |
| *Cotyledon orbiculata* | **Sp.77** |
| *Crassula atropurperea* | **Sp.78** |
| *Crassula capensis* | **Sp.79** |
| *Crassula capitella* | **Sp.80** |
| *Crassula congesta* | **Sp.81** |
| *Crassula dichotoma* | **Sp.82** |
| *Crassula expansa* | **Sp.83** |
| *Crassula muscosa* | **Sp.84** |
| *Crassula subaphylla* | **Sp.85** |
| *Curio radicans* | **Sp.86** |
| *Cyanella hyacinthiodes* | **Sp.87** |
| *Cyanella lutea* | **Sp.88** |
| *Cynanchum viminale* | **Sp.89** |
| *Cyperus longus* | **Sp.90** |
| *Cyphia* sp. | **Sp.91** |
| *Cyphia sylvatica* | **Sp.92** |
| *Cyphia volubilis* | **Sp.93** |
| *Cyrtanthus ventricosus* | **Sp.94** |
| *Cysticapnos vesicaria* | **Sp.95** |
| *Daucus carota* | **Sp.96** |
| Dead | **Sp.97** |
| *Delosperma peersii* | **Sp.98** |
| *Diascia bicolor* | **Sp.99** |
| *Diascia capensis* | **Sp.100** |

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|---|---|
| *Diascia capsularis* | **Sp.101** |
| *Diascia elongata* | **Sp.102** |
| *Diascia longicornis* | **Sp.103** |
| *Didelta spinosa* | **Sp.104** |
| *Digitaria eriantha* | **Sp.105** |
| *Dimorphotheca nudicaulis* | **Sp.106** |
| *Dimorphotheca pluvialis* | **Sp.107** |
| *Dimorphotheca sinuata* | **Sp.108** |
| *Dischisma ciliatum* | **Sp.109** |
| *Dittrichia graveolens* | **Sp.110** |
| *Dodonaea viscosa* | **Sp.111** |
| *Drimia capensis* | **Sp.112** |
| *Drimia elata* | **Sp.113** |
| *Drosanthemum hispidum* | **Sp.115** |
| *Drosanthemum lique* | **Sp.116** |
| *Drosanthemum montaguense* | **Sp.117** |
| *Drosanthemum praecultum* | **Sp.118** |
| *Echium plantagineum* | **Sp.119** |
| *Ehrharta calycina* | **Sp.120** |
| *Ehrharta erecta* | **Sp.121** |
| *Ehrharta longiflora* | **Sp.122** |
| *Ehrharta villosa* | **Sp.123** |
| *Elytropappus rhinocerotis* | **Sp.124** |
| *Enneapogon scaber* | **Sp.125** |
| *Enneapogon* sp. | **Sp.126** |
| *Erepsia ramosa* | **Sp.127** |
| *Erica cerinthoides* | **Sp.128** |
| *Erica hirta* | **Sp.129** |
| *Erica imbricata* | **Sp.130** |
| *Erica paniculata* | **Sp.131** |
| *Eriocephalus africanus* | **Sp.132** |
| *Eriocephalus ericoides* | **Sp.133** |
| *Eriospermum capense* | **Sp.134** |
| *Eriospermum lanceifolium* | **Sp.135** |
| *Eriospermum lanuginosum* | **Sp.136** |
| *Erodium moschatum* | **Sp.137** |
| *Euclea undulata* | **Sp.138** |
| *Euphorbia burmannii* | **Sp.139** |
| *Euphorbia hamata* | **Sp.140** |
| *Euphorbia mammillaris* | **Sp.141** |
| *Euphorbia mauritanica* | **Sp.142** |
| *Euphorbia tuberosa* | **Sp.143** |
| *Euryops abrotanifolius* | **Sp.144** |
| *Felicia echinata* | **Sp.145** |
| *Felicia filifolia* | **Sp.146** |
| *Felicia* sp. | **Sp.147** |
| *Ferraria* sp. | **Sp.148** |
| *Ficinia nigrescens* | **Sp.149** |
| *Ficinia radiata* | **Sp.150** |
| *Fumaria muralis* | **Sp.151** |
| *Galenia fruticosa* | **Sp.152** |
| *Galenia papulosa* | **Sp.153** |
| *Galium capense* | **Sp.154** |
| *Galium* sp. | **Sp.155** |
| *Galium tomentosum* | **Sp.156** |
| *Gazania krebsiana* | **Sp.157** |
| *Geissorhiza aspera* | **Sp.158** |
| *Gladiolus carneus* | **Sp.159** |
| *Gladiolus venustus* | **Sp.160** |
| *Glottiphyllum carnosum* | **Sp.161** |
| *Gnaphalium capense* | **Sp.162** |
| *Gnaphalium declinatum* | **Sp.163** |
| *Gnaphalium pauciflorum* | **Sp.164** |
| *Gnaphalium* sp. | **Sp.165** |
| *Gomphocarpus* sp. | **Sp.166** |
| *Gorteria diffusa* | **Sp.167** |
| *Gorteria personata* | **Sp.168** |
| *Gymnodiscus capillaris* | **Sp.169** |
| *Haemanthus sanguineus* | **Sp.170** |
| *Haworthia arachnoidea* | **Sp.171** |
| *Helichrysum cymosum* | **Sp.172** |
| *Helichrysum moeserianum* | **Sp.173** |
| *Helichrysum petiolare* | **Sp.174** |
| *Helichrysum* sp. | **Sp.175** |
| *Helichrysum teretifolium* | **Sp.176** |
| *Heliophila africana* | **Sp.177** |
| *Heliophila variabilis* | **Sp.178** |
| *Helminthotheca echioides* | **Sp.179** |
| *Hemimeris racemosa* | **Sp.180** |
| *Hemimeris sabulosa* | **Sp.181** |
| *Hereroa aspera* | **Sp.182** |
| *Hereroa fimbriata* | **Sp.183** |
| *Hereroa latepetala* | **Sp.184** |
| *Hermannia scabra* | **Sp.185** |
| *Hesperantha radiata* | **Sp.186** |
| *Hippia frutescens* | **Sp.187** |
| *Hoplophyllum spinosum* | **Sp.188** |
| *Hordeum murinum* | **Sp.189** |
| *Hyparrhenia hirta* | **Sp.190** |
| *Hypochaeris radicata* | **Sp.191** |
| *Ilex mitis* | **Sp.192** |
| *Isoetes capensis* | **Sp.193** |
| *Ixia polystachya* | **Sp.194** |
| *Lachanalia mutabilis* | **Sp.195** |
| *Lachanalia orchioides* | **Sp.196** |
| *Lachanalia pallida* | **Sp.197** |
| *Lachanalia* sp. | **Sp.198** |
| *Lampranthus* sp. | **Sp.199** |
| *Lampranthus uniflorus* | **Sp.200** |
| *Lapeirousia jacquinii* | **Sp.201** |
| *Lebeckia contaminata* | **Sp.202** |
| *Lebeckia sepiaria* | **Sp.203** |
| *Lebeckia* sp. | **Sp.204** |
| *Leipoldtia schultzei* | **Sp.205** |
| *Lepidium africanum* | **Sp.206** |
| *Lepidium didymum* | **Sp.207** |
| *Lessertia frutescens* | **Sp.208** |
| *Leucadendron lanigerum* | **Sp.209** |
| *Leucadendron rubrum* | **Sp.210** |
| *Leucadendron sessile* | **Sp.211** |
| *Leysera gnaphalodes* | **Sp.212** |
| *Lichtensteinia lacera* | **Sp.213** |
| *Licthtensteinia trifida* | **Sp.214** |
| *Lobelia setacea* | **Sp.215** |
| *Lobostemon argenteus* | **Sp.216** |
| *Lobostemon fruticosus* | **Sp.217** |
| *Lobostemon glaucophyllus* | **Sp.218** |
| *Lycium barbarum* | **Sp.219** |
| *Lycium cinereum* | **Sp.220** |
| *Lycium ferocissimum* | **Sp.221** |

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|---|---|
| *Lycium sp.* | **Sp.222** |
| *Malephora lutea* | **Sp.223** |
| *Malephora purpureo-crocea* | **Sp.224** |
| *Malva arborea* | **Sp.225** |
| *Manulea praeterita* | **Sp.226** |
| *Melasphaerula graminea* | **Sp.227** |
| *Melolobium aethiopicum* | **Sp.228** |
| *Melolobium candicans* | **Sp.229** |
| *Mesembryanthemum nodiflorum* | **Sp.230** |
| *Mesembryanthemum crystallinum* | **Sp.231** |
| *Mesembryanthemum guerichianum* | **Sp.232** |
| *Mesembryanthemum junceum* | **Sp.233** |
| *Mesembryanthemum noctiflora* | **Sp.234** |
| *Mesembryanthemum splendens* | **Sp.235** |
| *Mesembryanthemum vaginatum* | **Sp.236** |
| *Micranthus plantagineus* | **Sp.237** |
| *Microdon dubius* | **Sp.238** |
| *Microdon orbicularis* | **Sp.239** |
| *Microloma sagittatum* | **Sp.240** |
| *Montinia caryophyllacea* | **Sp.241** |
| *Moraea fugax* | **Sp.242** |
| *Moraea gawleri* | **Sp.243** |
| *Moraea minuata* | **Sp.244** |
| *Moraea nana* | **Sp.245** |
| *Moraea sp.* | **Sp.246** |
| *Moraea speciosa* | **Sp.247** |
| *Muraltia heisteria* | **Sp.248** |
| *Muraltia spinosa* | **Sp.249** |
| *Nemesia barbata* | **Sp.250** |
| *Nemesia ligulata* | **Sp.251** |
| *Nenax hirta* | **Sp.252** |
| *Nenax microphylla* | **Sp.253** |
| *Olea europaea* | **Sp.254** |
| *Oncosiphon grandiflorum* | **Sp.255** |
| *Oncosiphon piluliferum* | **Sp.256** |
| *Ornithogalum thyrsoides* | **Sp.257** |
| *Orthinogalum dubium* | **Sp.258** |
| *Osteospermum clandestinum* | **Sp.259** |
| *Osteospermum moniliferum* | **Sp.260** |
| *Osteospermum scariosum* | **Sp.261** |
| *Osteospermum sinuatum* | **Sp.262** |
| *Otholobium hirtum* | **Sp.263** |
| *Otholobium sp.* | **Sp.264** |
| *Othonna cylindrica* | **Sp.265** |
| *Oxalis corniculata* | **Sp.266** |
| *Oxalis depressa* | **Sp.267** |
| *Oxalis eckloniana* | **Sp.268** |
| *Oxalis flava* | **Sp.269** |
| *Oxalis glabra* | **Sp.270** |
| *Oxalis hirta* | **Sp.271** |
| *Oxalis luteola* | **Sp.272** |
| *Oxalis obtusa* | **Sp.273** |
| *Oxalis pes-caprae* | **Sp.274** |
| *Oxalis polyphylla* | **Sp.275** |
| *Oxalis sp.* | **Sp.276** |
| *Parietaria judaica* | **Sp.277** |
| *Passerina corymbosa* | **Sp.278** |
| *Peersia frithii* | **Sp.279** |
| *Pelargonium candicans* | **Sp.280** |
| *Pelargonium lobatum* | **Sp.281** |
| *Pelargonium sp.* | **Sp.282** |
| *Pelargonium triste* | **Sp.283** |
| *Pellaea pteroides* | **Sp.284** |
| *Pennisetum macrourum* | **Sp.285** |
| *Pennisetum setaceum* | **Sp.286** |
| *Pentameris airoides* | **Sp.287** |
| *Pentameris sp.* | **Sp.288** |
| *Pentzia incana* | **Sp.289** |
| *Pentzia sp.* | **Sp.290** |
| *Phalaris minor* | **Sp.291** |
| *Pharnaceum elongatum* | **Sp.292** |
| *Pharnaceum pussilum* | **Sp.293** |
| *Phylica villosa* | **Sp.294** |
| *Pinus pinaster* | **Sp.295** |
| *Polygala garcinii* | **Sp.296** |
| *Polypogon viridis* | **Sp.297** |
| *Portulacaria afra* | **Sp.298** |
| *Prismatocarpus fruticosus* | **Sp.299** |
| *Prosopis glandulosa* | **Sp.300** |
| *Protea repens* | **Sp.301** |
| *Pteronia aspera* | **Sp.302** |
| *Pteronia empetrifolia* | **Sp.303** |
| *Pteronia incana* | **Sp.304** |
| *Pteronia pallens* | **Sp.305** |
| *Pteronia paniculatus* | **Sp.306** |
| *Pteronia succulenta* | **Sp.307** |
| *Pterygodium catholicum* | **Sp.308** |
| *Raphanus raphanistrum* | **Sp.309** |
| *Restio capensis* | **Sp.310** |
| *Rhigozum obovatum* | **Sp.311** |
| *Roepera morgsana* | **Sp.312** |
| *Romulea hirsuta* | **Sp.313** |
| *Rumex sp.* | **Sp.314** |
| *Ruschia approximata* | **Sp.315** |
| *Ruschia bipapillitata* | **Sp.316** |
| *Ruschia caroli* | **Sp.317** |
| *Ruschia cradockensis* | **Sp.114** |
| *Ruschia diversifolia* | **Sp.318** |
| *Ruschia geminiflora* | **Sp.319** |
| *Ruschia pungens* | **Sp.320** |
| *Ruschia sp.* | **Sp.321** |
| *Ruschia spinosa* | **Sp.322** |
| *Ruschiella lunulata* | **Sp.323** |
| *Salsola aphylla* | **Sp.324** |
| *Salsola kali* | **Sp.325** |
| *Salvia africana* | **Sp.326** |
| *Salvia chamelaeagnea* | **Sp.327** |
| *Salvia sp.* | **Sp.328** |
| *Satyrium erectum* | **Sp.329** |
| *Searsia angustifolia* | **Sp.330** |
| *Searsia dissecta* | **Sp.331** |
| *Searsia incisa* | **Sp.332** |
| *Searsia rehmanniana* | **Sp.333** |
| *Searsia rosmarinifolia* | **Sp.334** |
| *Searsia tomentosa* | **Sp.335** |
| *Searsia undulata* | **Sp.336** |
| *Selago corymbosa* | **Sp.337** |
| *Senecio arenarius* | **Sp.338** |
| *Senecio burchelli* | **Sp.339** |
| *Senecio erosus* | **Sp.340** |

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|---|---|
| *Senecio inaequidens* | **Sp.341** |
| *Senecio pterophorus* | **Sp.342** |
| *Senecio pubigerus* | **Sp.343** |
| *Senecio radicans* | **Sp.344** |
| *Senecio rigidus* | **Sp.345** |
| *Seriphium plumosum* | **Sp.346** |
| *Serruria dodii* | **Sp.347** |
| *Sparaxis villosa* | **Sp.348** |
| *Spartium junceum* | **Sp.349** |
| *Spergula arvensis* | **Sp.350** |
| *Stipa capensis* | **Sp.351** |
| *Stipagrostis ciliata* | **Sp.352** |
| *Stoebe* sp. | **Sp.353** |
| *Struthiola ciliata* | **Sp.354** |
| *Tamarix ramosissima* | **Sp.355** |
| *Tetraena chrysopteros* | **Sp.356** |
| *Tetragonia fruticosa* | **Sp.357** |
| *Tetragonia rosea* | **Sp.358** |
| *Tetraria* sp. | **Sp.359** |
| *Tetraria ustulata* | **Sp.360** |
| *Torilis arvensis* | **Sp.361** |
| *Trachyandra divaricata* | **Sp.362** |
| *Trachyandra muricata* | **Sp.363** |
| *Trachyandra paniculata* | **Sp.364** |
| *Troglophyton* sp. | **Sp.365** |
| *Tulista pumila* | **Sp.366** |
| *Tylecodon paniculata* | **Sp.367** |
| *Ursinia anthemoides* | **Sp.368** |
| *Ursinia nana* | **Sp.369** |
| *Ursinia sericea* | **Sp.370** |
| *Urtica urens* | **Sp.371** |
| *Vellereophyton dealbatum* | **Sp.372** |
| *Wachendorfia paniculata* | **Sp.373** |
| *Wiborgia obcordata* | **Sp.374** |
| *Xiphotheca lanceolata* | **Sp.375** |
| *Zaluzianskya pusilla* | **Sp.376** |

## Appendix N

Growth forms of plant species by number assigned in Appendix M.

| | |
|---|---|
| **1** | shrub leaf-s evergreen |
| **2** | shrub non-s evergreen |
| **3** | shrub non-s evergreen |
| **4** | shrub non-s evergreen |
| **5** | shrub non-s evergreen |
| **6** | shrub non-s evergreen |
| **7** | geophyte non-s deciduous |
| **8** | geophyte non-s deciduous |
| **9** | geophyte non-s deciduous |
| **10** | geophyte non-s deciduous |
| **11** | shrub leaf-s evergreen |
| **12** | geophyte non-s deciduous |
| **13** | shrub non-s evergreen |
| **14** | shrub leaf-s evergreen |
| **15** | shrub non-s evergreen |
| **16** | shrub non-s evergreen |
| **17** | therophyte non-s deciduous |
| **18** | therophyte non-s deciduous |
| **19** | therophyte non-s deciduous |
| **20** | therophyte non-s deciduous |
| **21** | shrub non-s evergreen |
| **22** | shrub non-s evergreen |
| **23** | shrub non-s evergreen |
| **24** | hemicryptophyte non-s evergreen |
| **25** | shrub non-s evergreen |
| **101** | therophyte non-s deciduous |
| **102** | therophyte non-s deciduous |
| **103** | therophyte non-s deciduous |
| **104** | shrub leaf-s deciduous |
| **105** | hemicryptophyte non-s evergreen |
| **106** | geophyte non-s deciduous |
| **107** | therophyte non-s deciduous |
| **108** | therophyte non-s deciduous |
| **109** | shrub non-s evergreen |
| **110** | therophyte non-s deciduous |
| **111** | shrub non-s evergreen |
| **112** | geophyte non-s deciduous |
| **113** | geophyte non-s deciduous |
| **114** | shrub leaf-s evergreen |
| **115** | shrub leaf-s evergreen |
| **116** | shrub leaf-s evergreen |
| **117** | shrub leaf-s evergreen |
| **118** | shrub leaf-s evergreen |
| **119** | therophyte non-s deciduous |
| **120** | hemicryptophyte non-s evergreen |
| **121** | hemicryptophyte non-s evergreen |
| **122** | hemicryptophyte non-s evergreen |
| **123** | hemicryptophyte non-s evergreen |
| **124** | shrub non-s evergreen |
| **125** | hemicryptophyte non-s evergreen |
| **201** | geophyte non-s deciduous |
| **202** | shrub non-s deciduous |
| **203** | shrub non-s deciduous |
| **204** | shrub non-s deciduous |
| **205** | shrub leaf-s evergreen |
| **206** | shrub non-s evergreen |
| **207** | shrub leaf-s evergreen |
| **208** | shrub non-s evergreen |
| **209** | shrub non-s evergreen |
| **210** | shrub non-s evergreen |
| **211** | shrub non-s evergreen |
| **212** | shrub non-s evergreen |
| **213** | shrub non-s deciduous |
| **214** | shrub non-s deciduous |
| **215** | shrub non-s evergreen |
| **216** | shrub non-s evergreen |
| **217** | shrub non-s evergreen |
| **218** | shrub non-s evergreen |
| **219** | shrub non-s deciduous |
| **220** | shrub non-s deciduous |
| **221** | shrub non-s deciduous |
| **222** | shrub non-s deciduous |
| **223** | shrub leaf-s evergreen |
| **224** | shrub leaf-s evergreen |
| **225** | shrub non-s evergreen |
| **301** | shrub non-s evergreen |
| **302** | shrub non-s evergreen |
| **303** | shrub non-s evergreen |
| **304** | shrub non-s evergreen |
| **305** | shrub non-s evergreen |
| **306** | shrub non-s evergreen |
| **307** | shrub leaf-s evergreen |
| **308** | geophyte non-s deciduous |
| **309** | therophyte non-s deciduous |
| **310** | shrub non-s evergreen |
| **311** | shrub non-s deciduous |
| **312** | shrub leaf-s deciduous |
| **313** | shrub non-s evergreen |
| **314** | shrub non-s evergreen |
| **315** | shrub leaf-s evergreen |
| **316** | shrub leaf-s evergreen |
| **317** | shrub leaf-s evergreen |
| **318** | shrub leaf-s evergreen |
| **319** | shrub leaf-s evergreen |
| **320** | shrub leaf-s evergreen |
| **321** | shrub leaf-s evergreen |
| **322** | shrub leaf-s evergreen |
| **323** | shrub leaf-s evergreen |
| **324** | shrub non-s evergreen |
| **325** | therophyte leaf-s deciduous |

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|---|---|
| **26** | shrub non-s evergreen |
| **27** | shrub non-s evergreen |
| **28** | shrub non-s evergreen |
| **29** | shrub non-s evergreen |
| **30** | shrub non-s evergreen |
| **31** | shrub non-s evergreen |
| **32** | shrub non-s evergreen |
| **33** | shrub non-s evergreen |
| **34** | shrub non-s deciduous |
| **35** | shrub non-s deciduous |
| **36** | shrub non-s deciduous |
| **37** | shrub non-s deciduous |
| **38** | shrub non-s deciduous |
| **39** | shrub non-s deciduous |
| **40** | shrub non-s deciduous |
| **41** | shrub non-s evergreen |
| **42** | shrub non-s evergreen |
| **43** | shrub non-s evergreen |
| **44** | shrub leaf-s evergreen |
| **45** | therophyte non-s deciduous |
| **46** | geophyte non-s deciduous |
| **47** | geophyte non-s deciduous |
| **48** | geophyte non-s deciduous |
| **49** | shrub non-s evergreen |
| **50** | shrub non-s evergreen |
| **51** | therophyte non-s deciduous |
| **52** | therophyte non-s deciduous |
| **53** | therophyte non-s deciduous |
| **54** | therophyte non-s deciduous |
| **55** | shrub leaf-s deciduous |
| **126** | hemicryptophyte non-s evergreen |
| **127** | shrub leaf-s evergreen |
| **128** | shrub non-s evergreen |
| **129** | shrub non-s evergreen |
| **130** | shrub non-s evergreen |
| **131** | shrub non-s evergreen |
| **132** | shrub non-s evergreen |
| **133** | shrub non-s evergreen |
| **134** | geophyte non-s deciduous |
| **135** | geophyte non-s deciduous |
| **136** | geophyte non-s deciduous |
| **137** | therophyte non-s deciduous |
| **138** | shrub non-s evergreen |
| **139** | shrub stem-s |
| **140** | shrub stem-s |
| **141** | shrub stem-s |
| **142** | shrub stem-s |
| **143** | shrub stem-s |
| **144** | shrub non-s evergreen |
| **145** | shrub non-s evergreen |
| **146** | shrub non-s evergreen |
| **147** | shrub non-s evergreen |
| **148** | geophyte non-s deciduous |
| **149** | hemicryptophyte non-s evergreen |
| **150** | hemicryptophyte non-s evergreen |
| **151** | therophyte non-s deciduous |
| **152** | shrub non-s deciduous |
| **153** | shrub non-s deciduous |
| **154** | shrub non-s evergreen |
| **155** | shrub non-s evergreen |
| **226** | therophyte non-s deciduous |
| **227** | geophyte non-s deciduous |
| **228** | geophyte non-s deciduous |
| **229** | shrub non-s evergreen |
| **230** | therophyte leaf-s deciduous |
| **231** | therophyte leaf-s deciduous |
| **232** | therophyte leaf-s deciduous |
| **233** | shrub stem-s |
| **234** | shrub leaf-s deciduous |
| **235** | shrub leaf-s evergreen |
| **236** | shrub stem-s |
| **237** | geophyte non-s deciduous |
| **238** | geophyte non-s deciduous |
| **239** | geophyte non-s deciduous |
| **240** | shrub non-s evergreen |
| **241** | shrub non-s evergreen |
| **242** | geophyte non-s deciduous |
| **243** | geophyte non-s deciduous |
| **244** | geophyte non-s deciduous |
| **245** | geophyte non-s deciduous |
| **246** | geophyte non-s deciduous |
| **247** | geophyte non-s deciduous |
| **248** | shrub non-s evergreen |
| **249** | shrub non-s evergreen |
| **250** | therophyte non-s deciduous |
| **251** | therophyte non-s deciduous |
| **252** | shrub non-s evergreen |
| **253** | shrub non-s evergreen |
| **254** | tree non-s evergreen |
| **255** | therophyte non-s deciduous |
| **326** | shrub non-s evergreen |
| **327** | shrub non-s evergreen |
| **328** | shrub non-s evergreen |
| **329** | geophyte non-s deciduous |
| **330** | shrub non-s evergreen |
| **331** | shrub non-s evergreen |
| **332** | shrub non-s evergreen |
| **333** | shrub non-s evergreen |
| **334** | shrub non-s evergreen |
| **335** | shrub non-s evergreen |
| **336** | shrub non-s evergreen |
| **337** | shrub non-s evergreen |
| **338** | therophyte non-s deciduous |
| **339** | shrub non-s evergreen |
| **340** | shrub non-s evergreen |
| **341** | shrub non-s evergreen |
| **342** | shrub non-s evergreen |
| **343** | shrub non-s evergreen |
| **344** | shrub leaf-s evergreen |
| **345** | shrub non-s evergreen |
| **346** | shrub non-s evergreen |
| **347** | shrub non-s evergreen |
| **348** | geophyte non-s deciduous |
| **349** | shrub non-s deciduous |
| **350** | therophyte non-s deciduous |
| **351** | therophyte non-s deciduous |
| **352** | hemicryptophyte non-s evergreen |
| **353** | shrub non-s evergreen |
| **354** | shrub non-s evergreen |
| **355** | tree non-s deciduous |

| | |
|---|---|
| **56** | shrub leaf-s deciduous |
| **57** | shrub non-s evergreen |
| **58** | shrub leaf-s evergreen |
| **59** | therophyte non-s deciduous |
| **60** | therophyte non-s deciduous |
| **61** | shrub non-s evergreen |
| **62** | shrub non-s evergreen |
| **63** | shrub non-s evergreen |
| **64** | shrub non-s evergreen |
| **65** | shrub non-s evergreen |
| **66** | shrub non-s evergreen |
| **67** | therophyte leaf-s deciduous |
| **68** | shrub non-s evergreen |
| **69** | shrub non-s evergreen |
| **70** | shrub non-s evergreen |
| **71** | shrub non-s evergreen |
| **72** | geophyte non-s deciduous |
| **73** | shrub non-s evergreen |
| **74** | hemicryptophyte non-s evergreen |
| **75** | therophyte non-s deciduous |
| **76** | therophyte non-s deciduous |
| **156** | shrub non-s evergreen |
| **157** | shrub non-s deciduous |
| **158** | geophyte non-s deciduous |
| **159** | geophyte non-s deciduous |
| **160** | geophyte non-s deciduous |
| **161** | shrub leaf-s evergreen |
| **162** | therophyte non-s deciduous |
| **163** | therophyte non-s deciduous |
| **164** | therophyte non-s deciduous |
| **165** | therophyte non-s deciduous |
| **166** | shrub non-s evergreen |
| **167** | therophyte non-s deciduous |
| **168** | therophyte non-s deciduous |
| **169** | therophyte non-s deciduous |
| **170** | geophyte non-s deciduous |
| **171** | shrub leaf-s evergreen |
| **172** | shrub non-s evergreen |
| **173** | shrub non-s evergreen |
| **174** | shrub non-s evergreen |
| **175** | shrub non-s evergreen |
| **176** | shrub non-s evergreen |
| **256** | therophyte non-s deciduous |
| **257** | geophyte non-s deciduous |
| **258** | geophyte non-s deciduous |
| **259** | therophyte non-s deciduous |
| **260** | shrub non-s evergreen |
| **261** | shrub non-s evergreen |
| **262** | shrub non-s deciduous |
| **263** | shrub non-s evergreen |
| **264** | shrub non-s evergreen |
| **265** | shrub leaf-s evergreen |
| **266** | geophyte non-s deciduous |
| **267** | geophyte non-s deciduous |
| **268** | geophyte non-s deciduous |
| **269** | geophyte non-s deciduous |
| **270** | geophyte non-s deciduous |
| **271** | geophyte non-s deciduous |
| **272** | geophyte non-s deciduous |
| **273** | geophyte non-s deciduous |
| **274** | geophyte non-s deciduous |
| **275** | geophyte non-s deciduous |
| **276** | geophyte non-s deciduous |
| **356** | shrub leaf-s deciduous |
| **357** | shrub leaf-s deciduous |
| **358** | shrub leaf-s deciduous |
| **359** | hemicryptophyte non-s evergreen |
| **360** | hemicryptophyte non-s evergreen |
| **361** | therophyte non-s deciduous |
| **362** | shrub leaf-s evergreen |
| **363** | shrub leaf-s evergreen |
| **364** | shrub leaf-s evergreen |
| **365** | therophyte non-s deciduous |
| **366** | shrub leaf-s evergreen |
| **367** | shrub stem-s |
| **368** | therophyte non-s deciduous |
| **369** | therophyte non-s deciduous |
| **370** | shrub non-s evergreen |
| **371** | therophyte non-s deciduous |
| **372** | shrub non-s evergreen |
| **373** | shrub non-s evergreen |
| **374** | shrub non-s deciduous |
| **375** | shrub non-s evergreen |
| **376** | therophyte non-s deciduous |

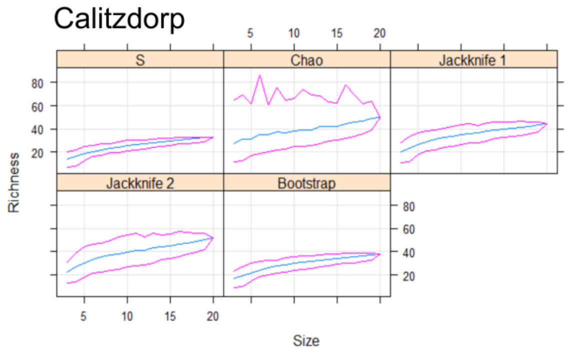
# Appendix O

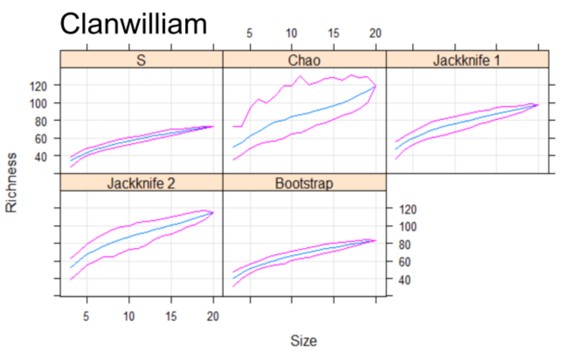
The ant species key, whereby each species is assigned a number, to identify ant species found and their abundance at each site.

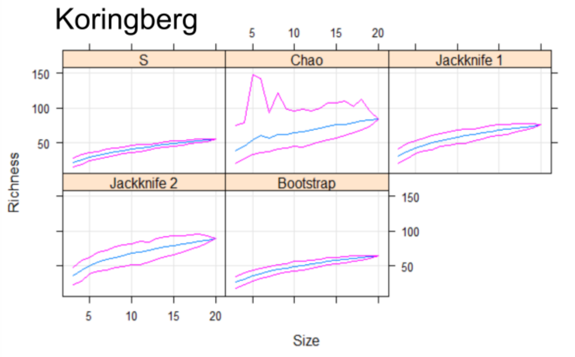
| | | | | | |
|---|---|---|---|---|---|
| *Anochetus levaillanti* | **Sp. 1** | *Dorylus* sp. | **Sp. 22** | *Ocymyrmex barbiger* | **Sp. 43** |
| *Anoplolepis custodiens* | **Sp. 2** | *Hagensia peringueyi* | **Sp. 23** | *Ophthalmopone hottentota* | **Sp. 44** |
| *Anoplolepis fallax* | **Sp. 3** | *Lepisiota capensis* | **Sp. 24** | *Pheidole capensis* | **Sp. 45** |
| *Anoplolepis rufescens* | **Sp. 4** | *Linepithema humile* | **Sp. 25** | *Pheidole tenuinodis* | **Sp. 46** |
| *Anoplolepis steingroeveri* | **Sp. 5** | *Meranoplus peringueyi* | **Sp. 26** | *Plagiolepis puncta* | **Sp. 47** |
| *Camponotus bianconni* | **Sp. 6** | *Mesoponera caffraria* | **Sp. 27** | *Tapinolepis trimenii* | **Sp. 48** |
| *Camponotus cinctellus* | **Sp. 7** | *Messor capensis* | **Sp. 28** | *Tapinoma albinase* | **Sp. 49** |
| *Camponotus cuneiscapus* | **Sp. 8** | *Messor denticornis* | **Sp. 29** | *Tapinoma arnoldi* | **Sp. 50** |
| *Camponotus fulvipilosus* | **Sp. 9** | *Messor striatifrons* | **Sp. 30** | *Technomyrmex pallipes* | **Sp. 51** |
| *Camponotus importunus* | **Sp. 10** | *Monomorium australe* | **Sp. 31** | *Tetramorium capense* | **Sp. 52** |
| *Camponotus maculatus* | **Sp. 11** | *Monomorium delagoense* | **Sp. 32** | *Tetramorium delagoense* | **Sp. 53** |
| *Camponotus mystaceus* | **Sp. 12** | *Monomorium esharre* | **Sp. 33** | *Tetramorium erectum* | **Sp. 54** |
| *Camponotus niveosetosus* | **Sp. 13** | *Monomorium exelsior* | **Sp. 34** | *Tetramorium glabratum* | **Sp. 55** |
| *Camponotus sericeus* | **Sp. 14** | *Monomorium fridae* | **Sp. 35** | *Tetramorium perinqueyi* | **Sp. 56** |
| *Camponotus vestitus* | **Sp. 15** | *Monomorium macrops* | **Sp. 36** | *Tetramorium pusillum* | **Sp. 57** |
| *Camponotus werthi* | **Sp. 16** | *Monomorium notulum* | **Sp. 37** | *Tetramorium rufescens* | **Sp. 58** |
| *Cardiocondyla shuckardi* | **Sp. 17** | *Monomorium pharaonis* | **Sp. 38** | *Tetramorium sericeiventre* | **Sp. 59** |
| *Crematogaster liengmei* | **Sp. 18** | *Monomorium rufulum* | **Sp. 39** | *Tetramorium signatum* | **Sp. 60** |
| *Crematogaster melanogaster* | **Sp. 19** | *Monomorium tablense* | **Sp. 40** | *Tetramorium solidinum* | **Sp. 61** |
| *Crematogaster schultzei* | **Sp. 20** | *Monomorium willowmorense* | **Sp. 41** | *Tetraponera emeryi* | **Sp. 62** |
| *Diplomorium longipenne* | **Sp. 21** | *Monomorium xanthognathum* | **Sp. 42** | | |

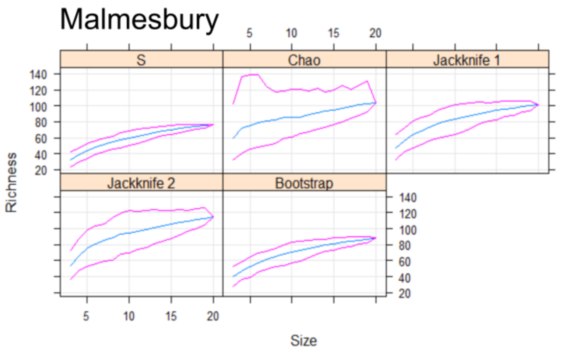
# Appendix P

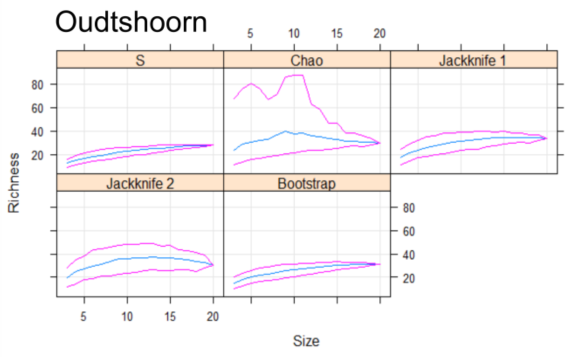
Observed plant species richness (S) and sample-based rarefaction curves along with estimated species richness curves (Chao, first and second order Jackknife, and Bootstrap indices) from twenty 20 m transects (10 from *Microhodotermes viator* nests, and 10 from the associated matrices) at each site.

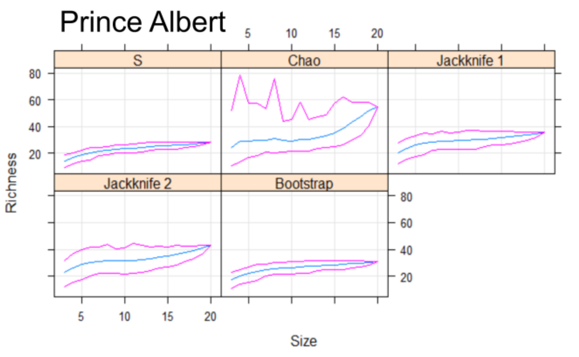

Calitzdorp

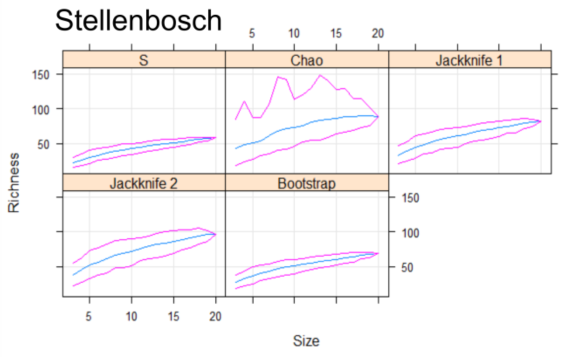

Clanwilliam

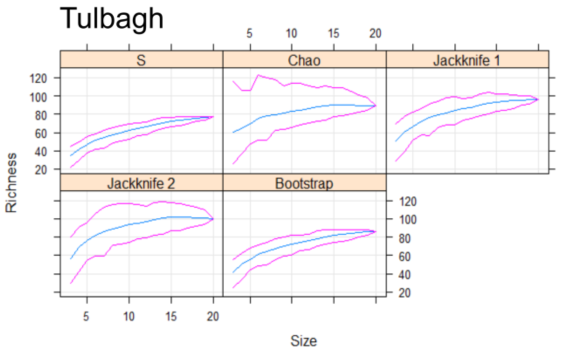

Koringberg

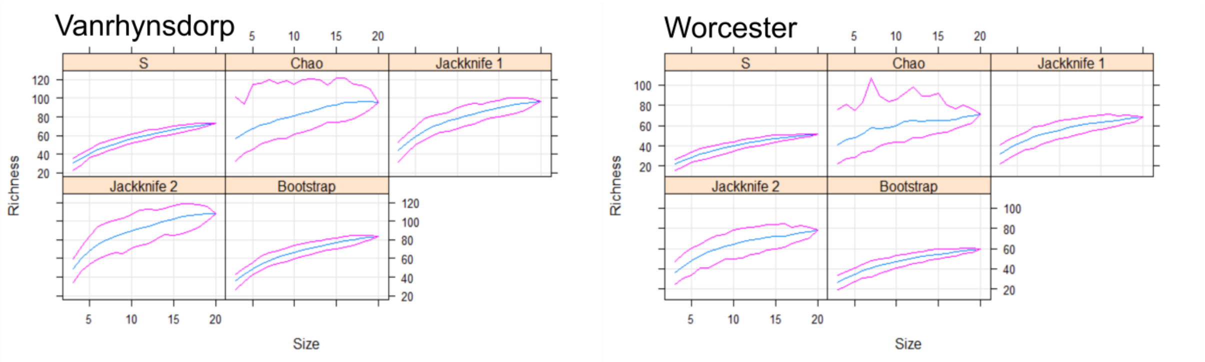

Malmesbury


Oudtshoorn

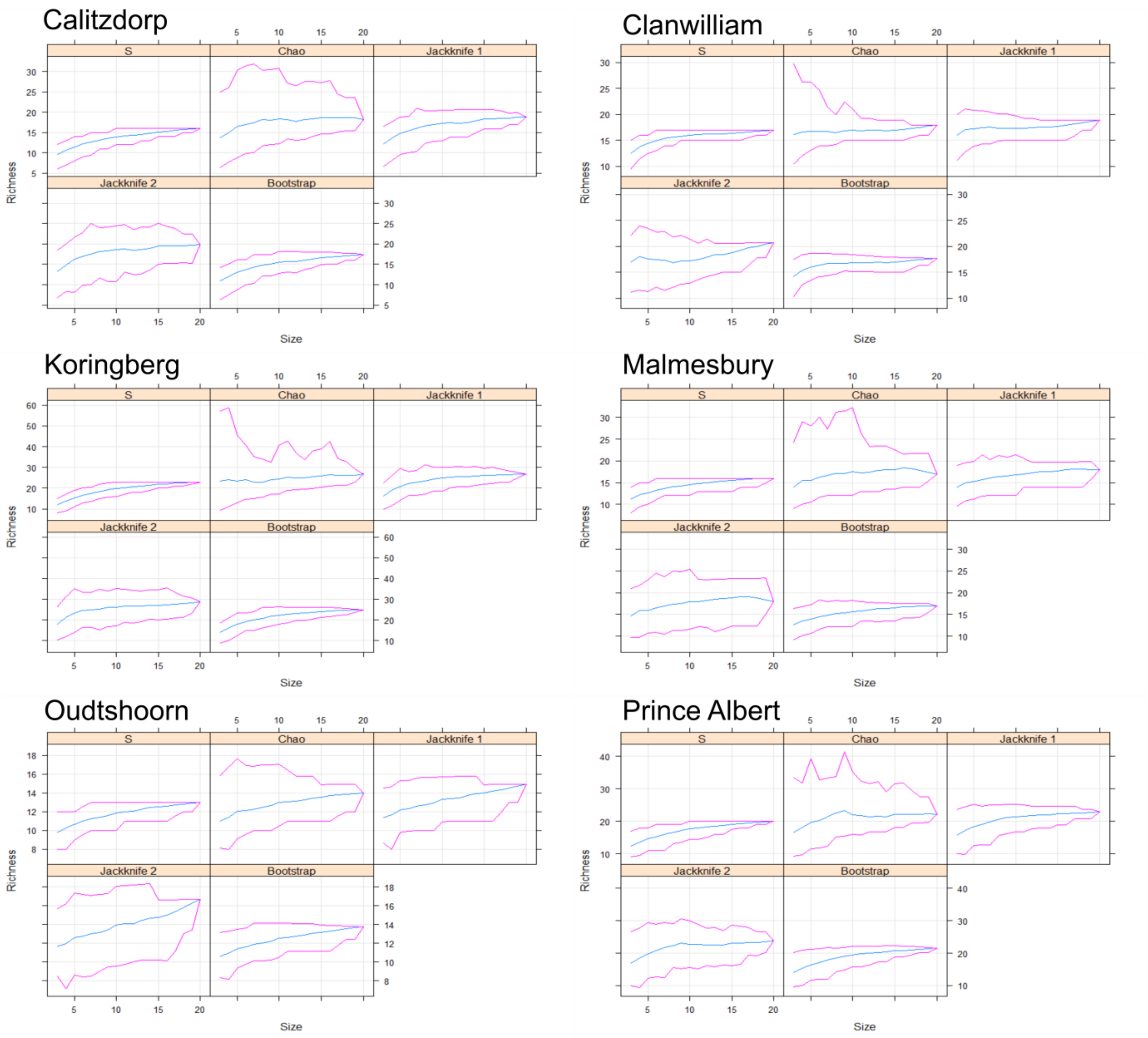

Prince Albert

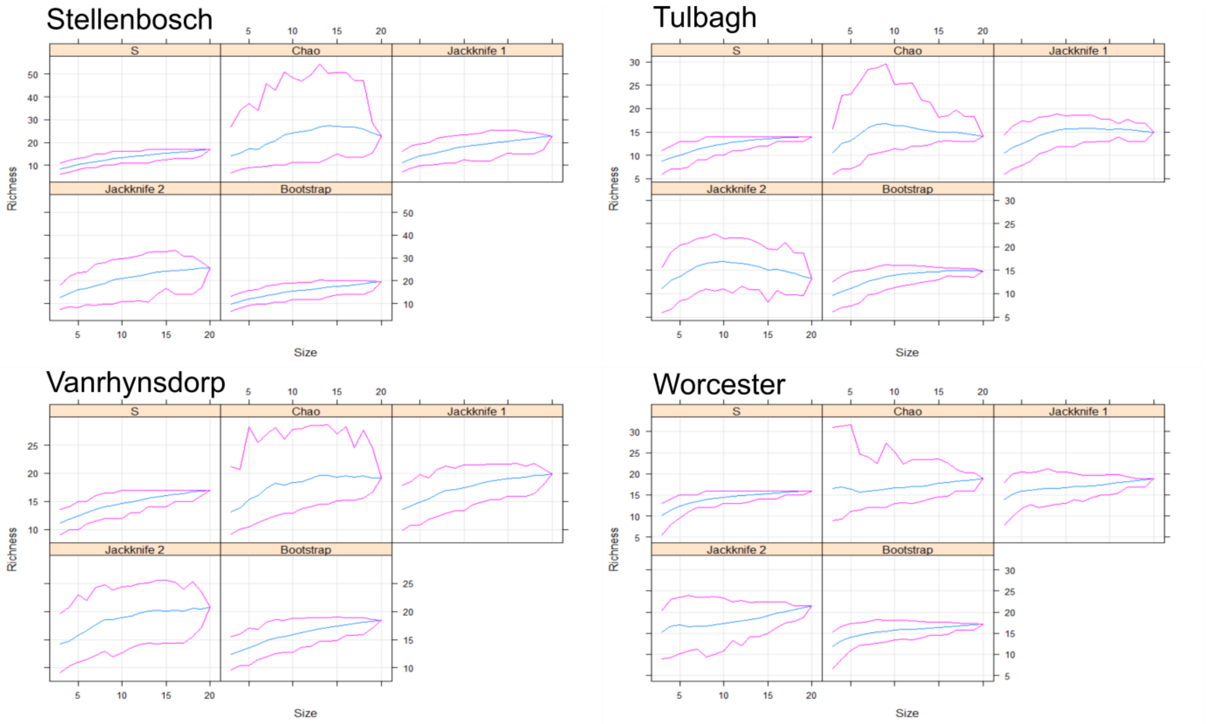

Stellenbosch


Tulbagh



Observed ant species richness (S) and sample-based rarefaction curves along with estimated species richness curves (Chao, first and second order Jackknife, and Bootstrap indices) from twenty 20 m transects (10 from *Microhodotermes viator* nests, and 10 from the associated matrices) at each site.




Stellenbosch
Tulbagh
Vanrhynsdorp
Worcester
S
Chao
Jackknife 1
Jackknife 2
Bootstrap
Richness
Size
5
10
15
20
10
20
30
40
50
25